Stuttgarter Beitr. Naturk. A | Neue Serie 1 | 2008

STUTTGARTER BEITRÄGE ZUR NATURKUNDE

A | Biologie

Fish names in Niebuhr 1775 ■ *Parablennius* from Australia and New Caledonia ■ Amphibians from Uruguay and Brazil ■ Terrestrial isopods of Greece ■ Pterothorax of Ephemeroptera, Odonata and Plecoptera ■ Revision of *Micrillus* ■ *Laena* from China

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Stuttgarter Beiträge zur Naturkunde

A (Biologie)

Stuttgart State Museum
Contributions to
Natural History

A (Biology)

Neue Serie
Band 1

Stuttgart, 2008

STAATL. MUSEUM FÜR NATURKUNDE
BIBLIOTHEK
STUTTGART

Allg-Z

Publisher

Herausgeber
© Staatliches Museum für Naturkunde Stuttgart

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Publication Date

Erscheinungsdatum
30. April 2008

Printer

Druck
Gulde Druck, Tübingen

ISSN 0341-0145

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Authorship, availability and validity of fish names described by Peter (Pehr) Simon Forsskål and Johann Christian Fabricius in the 'Descriptiones animalium' by Carsten Niebuhr in 1775 (Pisces)

Ronald Fricke

Abstract

The work of Peter (Pehr) Simon Forsskål, which has greatly influenced Mediterranean, African and Indo-Pacific ichthyology, has been published posthumously by Carsten Niebuhr in 1775. Forsskål left small sheets with manuscript descriptions and names of various fish taxa, which were later compiled and edited by Johann Christian Fabricius. Authorship, availability and validity of the fish names published by Niebuhr (1775a) are examined and discussed in the present paper. Several subsequent authors used Forsskål's fish descriptions to interpret, redescribe or rename fish species. These include Broussonet (1782), Bonnaterre (1788), Gmelin (1789), Walbaum (1792), Lacepède (1798–1803), Bloch & Schneider (1801), Geoffroy Saint-Hilaire (1809, 1827), Cuvier (1819), Rüppell (1828–1830, 1835–1838), Cuvier & Valenciennes (1835), Bleeker (1862), and Klunzinger (1871).

A total of 324 taxa in 114 families were treated by Niebuhr. Among these, a total of 153 new species (90 valid), and 5 new genera (all valid), were described. 26 additional nomina nuda were listed. A total of 126 names described in Niebuhr (1775a) are available, while 49 names are not available; 22 of these were subsequently made available. Though Niebuhr (1775a) is not consistently binominal, and would have to be rejected when strictly following Art. 11.4 of ICZN, it is here advised not to apply Art. 11.4 in this case to follow the principal aim of the Code, i.e. stability of nomenclature. Forsskål is the author of 68 available new taxa, while Fabricius authored 67; 22 taxa were subsequently made available by Bath, Bleeker, Bloch & Schneider, Bonnaterre, Cuvier, Fourmanoir & Guézé, Gmelin, Lacepède, Rüppell, and Walbaum. Four valid species require obligatory changes of their names: *Labeo vulgaris* Heckel, 1847 replaces *Labeo niloticus* (non Linnaeus, 1758, sensu Forsskål, 1775) (Cyprinidae); *Distichodus nefasch* (Bonnaterre [ex Forsskål], 1788) replaces *Distichodus niloticus* (Hasselquist, 1762) (Citharinidae); *Cheilodipterus arabicus* (Gmelin [ex Forsskål], 1789) replaces *Cheilodipterus lineatus* (non Linnaeus, 1758) sensu Forsskål in Niebuhr, 1775 (Apogonidae); *Symphodus ocellatus* (Linnaeus, 1758) replaces *Symphodus ocellaris* (Linnaeus, 1758) and *Symphodus ocellatus* (Forsskål in Niebuhr, 1775) (Labridae). 85 additional taxa require changes of authorship. In the case of Fabricius' authorship, and in 13 additional cases, where commonly used species names are threatened by unused names published in Niebuhr (1775a), applications to the International Commission on Zoological Nomenclature are required to stabilise current usage.

Keywords: Peter Simon Forsskål, Johann Christian Fabricius, fishes, nomenclature, authorship, availability, validity, ICZN, Egypt, Mediterranean Sea, Red Sea.

Zusammenfassung

Die Arbeit von Peter (Pehr) Simon Forsskål hat die Ichthyologie der Mittelmeers, Afrikas und des Indo-Pazifik stark beeinflusst; sie wurde posthum von Carsten Niebuhr im Jahre 1775 veröffentlicht. Forsskål hinterließ kleine Zettel mit Manuskriptbeschreibungen und Namen verschiedener Fischtaxa, die später von Johann Christian Fabricius zusammengestellt und herausgegeben wurden. In der vorliegenden Arbeit werden die Autorenschaft, Verfügbarkeit und Gültigkeit der von Niebuhr (1775a) publizierten Fischnamen untersucht und diskutiert. Mehrere spätere Autoren verwendeten Forsskåls Beschreibungen, um Fischarten neu zu interpretieren, wiederzubeschreiben oder umzubenennen. Hierzu zählen Broussonet (1782), Bonnaterre (1788), Gmelin (1789), Walbaum (1792), Lacepède (1798–1803), Bloch & Schneider (1801), Geoffroy Saint-Hilaire (1809, 1827), Cuvier (1819), Rüppell (1828–1830, 1835–1838), Cuvier & Valenciennes (1835), Bleeker (1862) und Klunzinger (1871).

Niebuhr behandelte insgesamt 324 Taxa in 114 Familien. Darunter befinden sich 153 Beschreibungen neuer Arten (davon 90 gültige Arten) und fünf neue Gattungen (alle gültig). Zusätzlich wurden 26 Nomina nuda aufgeführt. Insgesamt 126 der Artnamen sind verfügbar, während 49 Namen nicht verfügbar sind; 22 der letzteren Namen wurden später durch andere Autoren verfügbar gemacht. Obwohl die Nomenklatur in der Arbeit von Niebuhr (1775a) nicht durchgehend binominal ist und eigentlich bei strikter Anwendung von Art. 11.4 der Internationalen Nomenklaturregeln ungültig wäre, wird empfohlen, in diesem Fall nicht dem Art. 11.4 zu folgen, in Einklang mit dem Hauptziel der Nomenklaturregeln, der Stabilität der Nomenklatur. Forsskål ist der Autor von 68 verfügbaren neuen Taxa, Fabricius von 67; 22 Taxa wurden später durch Bath, Bleeker, Bloch & Schneider, Bonnaterre, Cuvier, Fourmanoir & Guézé, Gmelin, Lacepède, Rüppell und Walbaum verfügbar gemacht. Vier Artnamen müssen obligatorisch geändert werden: *Labeo vulgaris* Heckel, 1847 ersetzt *Labeo niloticus* (non Linnaeus, 1758, sensu Forsskål, 1775) (Cyprinidae); *Distichodus nefasch* (Bonnaterre [ex Forsskål], 1788) ersetzt *Distichodus niloticus* (Hasselquist, 1762) (Citharinidae); *Cheilodipterus arabicus* (Gmelin [ex Forsskål], 1789) ersetzt *Cheilodipterus lineatus* (non Linnaeus, 1758) sensu Forsskål in Niebuhr, 1775 (Apogonidae); und *Symphodus ocellatus* (Linnaeus, 1758) ersetzt *Symphodus ocellaris* (Linnaeus, 1758) und *Symphodus ocellatus* (Forsskål in Niebuhr, 1775) (Labridae). Außerdem bedürfen 85 weitere Taxa einer Änderung der Autorenschaft. Im Fall der Autorenschaft des Fabri-

CIUS sowie in 13 weiteren Fällen, in denen häufig verwendete Artnamen durch ältere Synonyme von FORSSKÅL-Arten bedroht werden, sind Anträge an die Nomenklaturkommission erforderlich.

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1 Introduction

The work of PETER (PEHR) SIMON FORSSKÅL has greatly influenced Mediterranean, African and Indo-Pacific ichthyology. FORSSKÅL was one of the so-called 'Linnaeus Apostles', who were sent out to discover the natural history of unknown parts of the world. During a Danish expedition in 1761–1763, FORSSKÅL was the first to collect and examine plants and animals, including fishes, in the Red Sea area. On his way there, he had the chance to work in the field in parts of the Mediterranean Sea and the Nile in Egypt, and compared his findings with previously published works (HASSELQUIST 1757, LINNAEUS 1758). This included numerous fishes he collected and started to describe. FORSSKÅL died in Yemen during the expedition, and the only survivor, CARSTEN NIEBUHR, returned with some collections and FORSSKÅL's manuscript notes, and published the fish descriptions posthumously (NIEBUHR 1775a).

We do not have much direct evidence about FORSSKÅL's work, the expedition and his findings. Most information is found in NIEBUHR's copies and translations; the original FORSSKÅL documents are either missing or lost. It is therefore essential to understand NIEBUHR's role.

CARSTEN NIEBUHR (Fig. 1) was born on 17 March 1733 in Lüdingworth-Westerende, Hadeln region, Hannover/Germany (NIEBUHR 1817, CARSTENS 1886, EHRENCRON-MÜLLER 1929, LOHMEIER 2002). He worked as a farmer in his early years, but managed to learn surveying, studied in Göttingen in 1757–1760, then moved to Denmark and accepted a position as Lieutenant Engineer in 1760. On the order of the King of Denmark FREDERIK V, he joined the expedition to 'Arabia Felix', i. e. Yemen, as the geographer. The other participants were Prof. PETER (PEHR) SIMON FORSSKÅL as a naturalist (biography see below), CHRISTIAN CARL CRAMER (KRAMER) (1732–1764) as a surgeon and naturalist (see EHRENCRON-MÜLLER 1925: 293–294), GEORG WILHELM BAURENFEIND as an artist and painter, Prof. FREDERIK (FRIDERICH) CHRISTIAN VON HAVEN (1727–1763) as the philologist and Arabist (see EHRENCRON-MÜLLER 1926: 450–451), and BERGRREN, a Danish soldier, who joined as the servant. The expedition left Copenhagen on 4 January 1761 (HANSEN 1965), travelled via Marseille (13 May–14 June 1761), Malta (14–20 June 1761), the Greek Archipelago (including Milos and Andros) and Smyrna (İzmir/Turkey; 20 June–30 July 1761) to Constantinopolis (İstanbul/Turkey; 30 July–26 Sep. 1761), then to Alexandria/Egypt. After spending a year in Egypt, ascending the Nile etc., they crossed the Red Sea and travelled along its eastern coast towards Yemen. The participants did not get along well with each other and had severe disputes even before reaching Alexandria. Especially VON HAVEN and FORSSKÅL were declared enemies; VON HAVEN even purchased arsenic in Constantinople and declared that he would find a way to get rid of FORSSKÅL during the expedition, while NIEBUHR wrote to the ministry he would be prepared to shoot down VON HAVEN if he would start poisoning the others (according to HANSEN 1965: 96). When they departed from Constantinople, they changed to local clothing pretending to be Muslim pilgrims. In Cairo, FORSSKÅL compiled a first version of his 'Descriptiones animalium' in spring 1762, and sent it back to Copenhagen; this version included spe-

Fig. 1. CARSTEN NIEBUHR, portrait (from TRAP 1868: 251).

cies observed in the Mediterranean Sea and in Egypt. The expedition then left Egypt by mule and small coastal vessels and finally arrived in Yemen in December 1762. Their orders required that they should stay for 2–3 years. Apparently, all of them soon got various diseases, probably diarrhoea, possibly also malaria. Within a year, the participants of the expedition died one by one under mysterious circumstances, VON HAVEN as the first in Móchha on 25 May 1763, then FORSSKÅL in Jerim on 11 July 1763; the others decided to leave Yemen on the next vessel from Móchha (Al-Mukhā/Yemen) towards Bombay, but BAURENFEIND and BERGGREN died on board the ship, and CRAMER passed away on 10 February 1764 in Bombay. CARSTEN NIEBUHR was the only survivor; he left India in the autumn of 1764, continued the expedition and returned via Muscat/Oman, Iran, Iraq, Syria, Cyprus, Palestine and Turkey to Denmark, where he arrived on 20 November 1767.

After his return, he immediately started publishing an expedition report (NIEBUHR 1772), and, posthumously, the work of his colleagues, especially FORSSKÅL. The fish specimens were described in NIEBUHR (1775a), and a few illustrations were published by NIEBUHR (1776). NIEBUHR received the full credit of a successful expedition, despite the fact that his companions had died en route. In 1768, he was appointed captain of the army; he retired in 1778 and moved back to Germany, where he continued his scientific career. NIEBUHR died on 26 April 1815 in Meldorf/Germany.

PETER (PEHR) SIMON FORSSKÅL (Fig. 2) (spelling of family name see FRIIS & THULIN 1984) was born on 11 January 1732 in Helsingfors (Helsinki); he studied in Uppsala in 1742–1753 and 1756–1759, was a scholar of CAROLUS LINNAEUS (CARL VON LINNÉ) and became a botanist (SPÄRCK 1963: 110–136; HILDEBRAND & MATINOLLI 1966: 359–362). From 1753–1756, he moved to Göttingen/Germany and became of student of JOHANN DAVID MICHAELIS, who originally had the idea of an expedition to Yemen. FORSSKÅL was a radical moderniser (in 1759, he had published 'Thoughts about the freedom of citizens'), and when he joined the Arabian expedition, he soon had disputes on this topic with VON HAVEN and others. We know what happened during the later expedition through the sparing notes in VON HAVEN's and FORSSKÅL's diaries, but mostly through NIEBUHR's reports. Mainly interested in botany and having collected and described many plants, had he previously also examined numerous fish, other vertebrate and invertebrate species. FORSSKÅL, however, had preserved relatively few specimens following a strong disagreement with a letter from the Danish government he received in Cairo. He knew that against his intentions he would have to return the specimens to Copenhagen. He did not trust the Danish government any longer. However, he would have been allowed to keep his notes and descriptions and take them back to Sweden (as a 'Linnaeus Apostle', he would have been expected to report directly to LINNAEUS himself). Therefore, he concentrated on taking notes and diagnoses of the fish species he found. At Jeddah, the expedition stayed for six weeks, and FORSSKÅL's official diary entries were very brief, lacking any detailed information about the town (FORSSKÅL 1950: 112), so that HANSEN (1965: 229) suspected that he was tired and not active any more. The contrary is true; we know from the Descriptiones animalium (FORSSKÅL in NIEBUHR 1775a) that most of the Red Sea fish descriptions were taken in Jeddah, and there were a total of 70 fish species described from there. At Jeddah, FORSSKÅL just did not bother to write entries for a diary that he had to send to Copenhagen. FORSSKÅL wrote an (illegal, as he was not allowed to give scientific information to anybody outside the Danish government) letter to CARL VON LINNÉ in Uppsala with information on some of his findings, and that his only aim was to stay alive long enough to present him his findings in person; if not, this would be a severe loss for science.

Fig. 2. PETER (PEHR) SIMON FORSSKÅL, portrait (Botanisk Centralbibliotek, Botanisk Have & Museum, Copenhagen).

Previously, he had sent a shipment of marine specimens from Constantinople (İstanbul) in 1761, which took two years to arrive in Copenhagen. The material was completely disintegrated on arrival, and had to be discarded (HANSEN 1965: 306). Another shipment from Egypt was severely damaged by pirates during its journey, and a parcel from Suez was lost on its way. More alcohol-preserved material had to be discarded during the trip on board the vessel from Jeddah to Al-Luhayya, as alcohol rapidly evaporated in the hot climate and the material started decaying, so that the smell became unbearable on board the small vessel.

In Lohaja (Al-Luhayya/Yemen), the first stop in 'Arabia felix' (Lucky Arabia/Yemen), the Danish expedition had temporarily a relatively good and happy time. Forsskål, who was mainly interested in botany and made long excursions into the desert, still found some time to work on his fish descriptions. However, he did not collect much material, apparently only a few small bottles with fishes in alcohol. This collection was sent to Al-Mukhā, while the expedition planned to spend the hot summer in the Yemeni mountains, but as they were all ill, they decided to visit Al-Mukhā immediately, which was, in the end, not a wise decision. The (small) remaining fish collection was inspected and mostly destroyed by a customs officer (Hansen 1965: 270–271), and the members of the expedition, including von Haven who was severely ill, had even problems with finding accommodation in town.

After the raid in Al-Mukhā and the death of Forsskål, the remaining material was taken by Niebuhr to Bombay and then shipped to Copenhagen via Tranquebar. During the long voyage, some material was destroyed by salt water or disintegration, and had to be discarded in Tranquebar. Ten parcels with Forsskål materials were received by Ascanius, curator of the natural history collection in Copenhagen (Hansen 1965: 309). Unfortunately, Ascanius did not curate the materials, but left the parcels unopened for several years. In 1765 Linnaeus asked the young zoologist Brünnich about the state of the collections, who informed him that they were still locked up by Ascanius and neither curated nor available for research (Hansen 1965: 309–310).

The remaining material was finally returned to Copenhagen and survived serious miscuration by Ascanius (Hansen 1965: 308–310). Brünnich, the new curator of the Copenhagen natural history collection, reopened Forsskål's parcels in 1772, sorted out the material which could still be used, and discarded rotten material. Unfortunately, since the bombardment of Copenhagen in 1807, the specimens were deposited in the magazine without curation and respiriting for another 30 years, and additional material was lost (Hansen 1965: 310–311). Today, only 99 specimens of fishes, exclusively consisting of the dried fish skins that Forsskål mainly collected in Jeddah, are remaining (Klausewitz & Nielsen 1965, Rasmussen 2002: 45). Types of Forsskål species in ZMUC are listed by Nielsen (1974). In addition, specimens collected by Forsskål were used for species descriptions by Brünnich 1768 (Hansen 1965: 310).

The work published by Niebuhr (1775a) is extremely inconsistent and full or errors; nevertheless, many fish species that are still considered valid were described in this work. The author has generally been given as Forsskål, but several names, diagnoses and descriptions were compiled subsequently, and Forsskål neither knew about this usage nor would have intended to name the genera and species that way. Therefore, authorship, availability and validity of the fish names published by Niebuhr (1775a) are examined and discussed in the present paper.

Acknowledgments

I would like to thank the following individuals for providing information about Forsskål's materials and history, and for discussing taxonomical questions and rules: William N. Eschmeyer (California Academy of Sciences, San Francisco, USA); Gerhard Falkner (SMNS); Peter R. Møller, Claus Nielsen, Jørgen G. Nielsen and Thomas Pape (ZMUC); Philippe Provençal (Århus University, Århus, Denmark); Stig T. Rasmussen (Det Kongelige Bibliotek, Copenhagen, Denmark). I am grateful to Sabine Petri (SMNS) who assisted with loans of rare books, and with historical research. Librarians of the Botanisk Centralbibliotek, Botanisk Have & Museum (Copenhagen, Denmark), National Library, University of Helsinki (Helsinki, Finland), the Science Library, Viikii University Campus (Helsinki, Finland), the Staats- und Universitätsbibliothek, Forschungsbibliothek (Göttingen, Germany), the Universitätsbibliothek, Christian-Albrechts-Universität (Kiel, Germany), and the Württembergi-

Tab. 1. Authors of nominal taxa of fishes based on Forsskål's descriptions.

Author	Name	Lifetime
Anonymus	Unknown Maltese father who provided a list of Maltese fishes during Forsskål's visit in La Valletta, 14–20 June 1761; he was called a 'learned friend' in Forsskål's diary	
Bleeker	Pieter Bleeker	1819–1878
Bloch	Marcus Elieser Bloch	1728–1799
Bonnaterre	Pierre Joseph Bonnaterre	1747(?)–1804
Fabricius	Johann Christian Fabricius	1745–1808
Forsskål	Peter (Pehr) Simon Forsskål	1732–1763
Gmelin	Johann Friedrich Gmelin	1748–1804
Klunzinger	Carl Benjamin Klunzinger	1834–1914
Lacepède	Bernard Etienne Germain de la Ville-sur-Illon, Comte de Lacepède	1756–1825
Niebuhr	Carsten Niebuhr	1733–1815
Rüppell	(Wilhelm Peter) Eduard (Simon) Rüppell	1794–1884
Schneider	Johann Gottlob Schneider	1750–1822
Valenciennes	Achille Valenciennes	1794–1865
Walbaum	Johann Julius Walbaum	1724–1799

sche Landesbibliothek (Stuttgart, Germany) gave access to rare literature and documents in their care. I appreciate the excellent work of FRIEDHELM KRUPP (Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main, Germany) and JØRGEN G. NIELSEN (ZMUC) who critically read the manuscript.

2 Methods

The authorship, availability and validity of fish names listed and described in NIEBUHR (1775a) are examined. For each of these taxa, the currently used name is given first; then, the original reference(s) of NIEBUHR (1775a) are quoted with exactly the same typesetting as in the original text, including errors. In the case of new taxa, the type locality, type materials, the genus and species names used by FORSSKÅL and FABRICIUS, and the Latinised Arabic names are given. Families are arranged according to NELSON (2006). In a 'Remarks' section, authorship, criteria of availability, validity, and eventual synonymies of subsequently described names based on FORSSKÅL's description, are discussed. The spelling of the name FORSSKÅL follows FRIIS & THULIN (1984), though the name was spelled 'FORSKÅL' in the original publication (NIEBUHR 1775a).

Type material and other FORSSKÅL material is listed if available; if no types or materials are known, they are omitted in the species accounts.

In accordance with the International Code on Zoological Nomenclature 'ICZN' (Anonymus 2007a), the aim of stability of nomenclature is accepted as the basic principle in the present paper; as far as possible, names of prevailing usage are retained. Changes of authorship of taxa originally described in NIEBUHR (1775a) are quoted here for nomenclatural discussion only and do not imply nomenclatural changes; such cases will be directed to ICZN for decision.

Authors of nominal taxa based on FORSSKÅL's descriptions are listed in Tab. 1.

For the discussion of Turkish fish species and their local names, FRICKE et al. (2007) is used as a standard reference. Some Arabic vernacular names as used by FORSSKÅL are given in modern Arabic characters by BAHEYELDIN (2002). Arabic characters of the quotations are not used in the present paper, but are replaced by '[..., Arabic name]'. Maltese fish names follow Anonymus (2007b).

Documents by C. NIEBUHR were examined in the Universitätsbibliothek der Christian-Albrechts-Universität Kiel (Signature 'Cod. MS. KB 314 – NIEBUHR Nachlass').

Geographical coordinates of frequently mentioned localities are listed in Tab. 2.

Tab. 2. Geographical coordinates of frequently mentioned localities.

Country	Locality	Coordinates
Egypt	Alexandria, Al-Iskandarīyah	31°12'N 29°54'E
Egypt	As-Suways	29°58'N 32°33'E
Egypt	Dumyāt	31°25'N 31°48'E
France	Marseille	43°18'N 5°22'E
Malta	La Valletta	35°54'N 14°31'E
Saudi Arabia	Jeddah, Juddah	21°30'N 39°12'E
Turkey	İzmir	38°25'N 27°09'E
Turkey	İstanbul	41°01'N 28°58'E
Yemen	Al-Luhayya	15°42'N 42°42'E
Yemen	Al-Mukhā	13°19'N 43°15'E

Acronyms of museum collections

BPBM Bernice P. Bishop Museum, Honolulu, Hawai'i, USA
HUJ Hebrew University of Jerusalem, Israel
NRM Naturhistoriska Riksmuseet, Stockholm, Sweden
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
USNM National Museum of Natural History, Smithsonian Institution, Washington D.C., USA
ZMUC Zoologisk Museum, Copenhagen, Denmark

3 Authorship and availability of FORSSKÅL's fish species

A total of 324 taxa in 114 families were treated by NIEBUHR (1775a). Among these, a total of 153 new species (90 valid), and 5 new genera (all valid), are described. 26 additional nomina nuda were listed. A total of 126 names described in NIEBUHR (1775a) are available, while 49 names are not available; 22 of these were subsequently made available.

A major problem is that NIEBUHR (1775a) is not consistently binominal, due to errors included by FABRICIUS (see below). Applying the Code strictly (ICZN, Art. 11.4), it would have to be rejected. However, parallel to the case of the botanical volume (FORSSKÅL in NIEBUHR 1775b; see FRIIS et al. 1984, GREUTER 1984), this would be disastrous for the stability of nomenclature, as numerous species would have to change their names. The primary aim of the Code is stability of nomenclature (see ICZN, preamble); Art. 11.4 is not meant to weaken this stability. Therefore, I do not advise to follow Art. 11.4 strictly in the case of FORSSKÅL in NIEBUHR's work, but to consider the work as mainly binominal, and to ignore the few non-binominal cases as errors which were not intended to be published as such, at least by FORSSKÅL.

FORSSKÅL's manuscript was far from ready for publication (HANSEN 1965: 314–315). He only had individual, small pieces of paper with field notes in minuscule writing intended for his own use (HANSEN 1965: 314–315; P. PROVENÇAL, Århus, personal communication, Jan. 2007). NIEBUHR (1792: 310–311) wrote: "After my return to Europe, I was intrusted with the task of publishing my friend's [FORSSKÅL's] posthumous papers. I then discovered a new loss which natural history had suffered by his death. He had been accustomed to write down his observations on small detached pieces of paper, which could not easily be preserved together. It is true, I found 1800 of these billets, which I endeavoured to reduce into order. But I could not help inferring from the chasms here and there, that many of them were lost. Whether it be or be not so, I have, however, presented to the public all that I could recover, in two Latin works, intitled, *Descriptiones Animalium,* 4*to Hafniæ,* 1775 [NIEBUHR 1775a]; and *Flora Arabica,* 4*to, ib.* 1775 [NIEBUHR 1775b]. These two works, written in Latin,

and in the manner and arrangement of *Linnæus*, are intended particularly for the use of the learned naturalist. To gratify readers of all classes, I shall here insert the most curious particular of the information contained in those works, and such as will serve to give the best ideas of the productions, common or peculiar, of the countries which we traversed. Although natural history was not my province, I had occasion to observe transiently many things respecting it. I shall, therefore, intermingle my own remarks, without distinguishing them as such; for the greater part of the whole is Mr Forskal's.". NIEBUHR, who as an engineer was not familiar with zoological systematics, and knew only German and Danish, but very little Latin and no Swedish, paid an enormous salary to an adviser on natural history, who had the difficult task of interpreting the meaning of FORSSKÅL's notes, with many Arabic names in both Arabic and Latin letters (PROVENÇAL 2002), some scientific names, other local names, diagnoses and descriptions. He apparently confused or misinterpreted some of them; or wanted to describe new species where FORSSKÅL's descriptions were not yet ready, and deliberately used the Arabic names as species names, which were only intended by FORSSKÅL as a proxy to be later replaced by a Latin equivalent (as described for the example of *Abu-defduf* by JORDAN & EVERMANN 1917: 33). However, there are obviously numerous misinterpretations and switching of names into the wrong column. The adviser was a strange man, and NIEBUHR was not really happy with his work (NIEBUHR 1817: 50–51); he was, however, able to translate FORSSKÅL's notes in Swedish into Latin language, and sort and copy the Latin parts of the diagnoses and descriptions. NIEBUHR was never able to check if the work of the adviser was correct.

Though NIEBUHR never published or mentioned the name of the adviser, a letter indicating his identity was found by the author of the present paper in NIEBUHR's documents in the archive of the library of the Christian-Albrechts-Universität Kiel. FORSSKÅL's travel itinerary was translated into German by JOHANN CHRISTIAN FABRICIUS (FABRICIUS 1776a), according to a letter by FABRICIUS dated 16 Jan. 1776 (FABRICIUS 1776b). This letter is a humble writing where FABRICIUS repeatedly expressed his hopes that this work would please NIEBUHR, in spite of the fact that the previous work did not. This is a strong evidence for FABRICIUS's earlier work on FORSSKÅL's manuscript notes and compilation of the 'Descriptiones Animalium' (NIEBUHR 1775a), a work which did not please NIEBUHR the year before. FABRICIUS, however, had been a logical choice, as he was the only German speaking LINNAEUS scholar who, living in Copenhagen during the winters of 1772–1775, was fluent in Danish and Swedish; this was easiest for NIEBUHR, who was only able to talk and correspond in German and Danish on his own account, and needed a translator for letters in any other language. FABRICIUS had previously (in 1764) worked with insect material in the FORSSKÅL collection (LATREILLE 1808: 401; HOPE 1845: III), which made him seem fit for the task of revising FORSSKÅL's natural history manuscripts. later, NIEBUHR found out that FABRICIUS was a 'strange fellow' (NIEBUHR 1817: 50–51), who apparently did not take much time in the task in spite of his high salary, and was probably more interested in his own scientific work on insects rather than the translation and compilation of FORSSKÅL's manuscript notes on fishes and other animals. The German translation of FORSSKÅL's travel itinerary (FABRICIUS 1776a) was neither well done, with a barely readable handwriting and many crossing-outs, and FABRICIUS doesn't seem to have wasted too much time on it either.

JOHANN CHRISTIAN FABRICIUS (Fig. 3) was born in Tønder/Denmark on 7 January 1745; he went to school in Altona (Hamburg) (HOPE 1845: I). FABRICIUS studied natural history in Copenhagen and Uppsala; as a scholar of LINNAEUS. From 1769–1775, Fabricius was extraordinary professor at the University of Copenhagen, spending the winters in Copenhagen and the summers in London (HOPE 1845: VIII). In 1775, he was appointed as professor of natural history, economics and finance at Kiel University, and moved to Kiel. Again, he spent winters in Kiel and summers in Paris and London. FABRICIUS was one of the founders of entomological systematics, and published several important works on the subject, including a general classification (FABRICIUS 1792–1794). He died in Kiel on 3 March 1808.

FORSSKÅL's natural history notes were not intended to be published in this provisional state, but merely to form the basis of future research and editing. Unfortunately, they were published in a crude and unedited way, and nu-

Fig. 3. JOHANN CHRISTIAN FABRICIUS, portrait (from HOPE 1845).

merous errors and misinterpretations were included; even the arrangement of the material does not follow a common logic, but is heterogeneous and can easily be misinterpreted (HANSEN 1965: 314–315). While the botanical descriptions and identifications were pretty accurate (FRIIS 1984), and FORSSKÅL already distinguished numerous new families, genera and species, the fish names and descriptions were rather crude, needing further study, and FORSSKÅL frequently misidentified Linnaean species judging from the identifications for Turkish common names, and from the descriptions of specimens from Marseille.

The authorship of the names is a complicated question. A key to this is the usage of Latin or Arabic names as species names. NIEBUHR (1775a: 16) wrote in his introduction that FORSSKÅL intended to give Arabic names transcribed (types in italics) and in their original version. In the index, species names were given inconsistently, like the example of 'Perca ROGAA; subnigra'. This means, that the genus is *Perca*; 'rogaa' is the Arabic name; and '*subnigra*' was originally meant as the species name. Though authors have used *Perca rogaa* as the species name, it might in fact have been *Perca subnigra* (with 'rogaa' as the Arabic name). As a rule, FORSSKÅL always used a Latin or Greek, or at least Latinised name when he intended to give a scientific name for a species, following LINNAEUS's (1758) example; the Arabic names are only an additional information on local names. If there is no Latin/Greek name available, then FORSSKÅL was not sure about the identity of the species and only identified the genus, given the local Arabic name in addition, to work on the problem at home and later eventually select a Latin or Greek scientific name. It is therefore concluded that Latin or Greek species names described in NIEBUHR (1775a) were selected by FORSSKÅL himself, while the use of Arabic or other local names is due to FABRICIUS's erroneous usage of these substitutes as species names.

Neither FORSSKÅL nor FABRICIUS in NIEBUHR usually gave reference to previous authors. If they used Linnaean names, we can be certain that they knew them, because a copy of LINNAEUS (1758) was the standard equipment of a natural history expedition in the late 18th century, and FORSSKÅL (a scholar of LINNAEUS) and FABRICIUS in NIEBUHR had it available as well (see NIEBUHR 1775a: 18). Linnaean names used by FORSSKÅL cannot be considered as independent descriptions even if dealing with different species; in the latter case, they are misidentifications. Numerous such misidentifications were found in Turkish species where local names are given, which are species-specific even in closely related commercial species and can now be used to identify the species.

Authorship is defined by ICZN, Art. 50. Unfortunately, Art. 50.1 is not unambiguous. From the sentence 'If a work is by more than one person but it is clear from the contents that only one of these is responsible for the name or act, then that person is the author; otherwise the author of the work is deemed to be the author of the name or act' would follow that NIEBUHR should be the author. Art. 50.1 strongly emphasises the 'Contents' of the work. The problem here is that the person 'who first published the work' is here not identical with the author of the names, and neither with the person who provided the field data basis for the description; these are often three different persons, or groups of persons. The 'person who first publishes the work' is clearly NIEBUHR; the authorship cannot be solved from the 'Contents', as not only FABRICIUS was not mentioned, but NIEBUHR also states an authorship (which here means field data source) mixed between himself and FORSSKÅL (FORSSKÅL's contribution is estimated at 50–60%); also included were names of Maltese fishes provided by an anonymous Maltese scientist. The third sentence of Art. 50.1 'If the author, or the person who publishes the work, cannot be determined from the contents, then the name or act is deemed to be anonymous', therefore implies an anonymous authorship. As we meanwhile know the authors from other sources, I do not consider this advisable.

The descriptions provided by FORSSKÅL and NIEBUHR were far from ready for publication; they were merely raw field data, on tiny pieces of paper in minuscule, barely readable handwriting. The mentioning of Arabic names in Arabic letters and in Roman transliteration was not a decision of naming species as such, but was part of the royal order for the expedition. Many such names were indicated as 'Arab.' (meaning Arabic), and often several names were given for one item. FABRICIUS was much more than a paid secretary to write the manuscript down; it was up to him to make decisions which items to describe as new species. In some cases, FORSSKÅL gave the scientific names and thus decided a taxon should be described as a new species; then I agree with FORSSKÅL as the author of the taxon. In many other cases, he left the scientific name open, and it was up to FABRICIUS to decide a description as new species, and to add the Arabic or other local name as scientific name. Most of the descriptions as we see them in the manuscript are the work of FABRICIUS, who did extensive research, though probably not seeing the specimens himself (however, we cannot be certain about this either, as FABRICIUS had access to FORSSKÅL insect material from the same collection at that time, provided by ASCANIUS); it took him about three years to work on these. In some cases, we know that FABRICIUS did additional literature research on papers which were not yet available to FORSSKÅL.

As a decision to change authorship on a broad scale would be premature in the present paper, I here leave the authorship generally in the status quo, as "Forsskål in Niebuhr, 1775", and discuss the nomenclatural situation afterwards; no nomenclatural changes should arise from this

paper in such cases, unless the case has been subsequently decided by the International Commission on Zoological Nomenclature.

It was assumed that BRÜNNICH (1768) might have used FORSSKÅL material from Marseille for his Ichthyologia Massiliensis; however, as FORSSKÅL's fish parcels and manuscript were unavailable at that time, and were only reopened in 1772, as BRÜNNICH wrote his 'Ichthyologia Massiliensis' while on visit to Vienna (BRÜNNICH 1768: XVI), and as no reference is given to either FORSSKÅL or his material or the Copenhagen collection at all, it can be concluded that BRÜNNICH's work is independent of FORSSKÅL's studies on fishes from Marseille.

Several later authors, however, used the work of NIEBUHR (1775a) to interpret, redescribe or rename fish species. These include BROUSSONET (1782), BONNATERRE (1788), GMELIN (1789), WALBAUM (1792), LACEPÈDE (1798–1803), BLOCH & SCHNEIDER (1801), GEOFFROY SAINT-HILAIRE (1809, 1827), CUVIER (1819), RÜPPELL (1828–1830, 1835–1838), CUVIER & VALENCIENNES (1835), BLEEKER (1862), and KLUNZINGER (1871). FORSSKÅL's work is of especial interest to science, as it not only includes the first known Red Sea fish fauna, but also the first fish faunal list from Malta, and the first list of marine fishes of western Turkey.

Though previously all taxa were attributed to the authorship of FORSSKÅL, he is only the author of 68 available new taxa, while FABRICIUS authored 67 (opinion of the present paper); 22 taxa were subsequently made available by BATH, BLEEKER, BLOCH & SCHNEIDER, BONNATERRE, CUVIER, FOURMANOIR & GUÉZÉ, GMELIN, LACEPÈDE, RÜPPELL and WALBAUM. Three species require obligatory changes of their names, 47 additional species require changes of authorship. Such cases cannot be decided in the present paper, but will be refered to the International Commission on Zoological Nomenclature for decision (see above). In 13 cases, where commonly used species names are threatened by unused names published in NIEBUHR (1775a), applications to the International Commission on Zoological Nomenclature are required to stabilise the current usage.

4 Fish taxa described by FORSSKÅL and FABRICIUS in NIEBUHR (1775a)

Petromyzontidae – Northern lampreys

Petromyzontidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "PETROMYZON *lampetra*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This record, a name only, is based on either of the two Mediterranean species of the family, *Petromyzon marinus* Linnaeus, 1758 or *Lampetra fluviatilis* (Linnaeus, 1758); as no diagnosis or local name was given, it cannot be assigned to generic or species level.

Scyliorhinidae – Cat sharks

Scyliorhinus canicula (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SQUALUS] *catulus*".

Locality: "Melita" (La Valletta/Malta). Maltese name: "Il rufetta".

Remarks: This record is based on *Squalus catulus* Linnaeus, 1758, a junior synonym of *Squalus canicula* Linnaeus, 1758, now named *Scyliorhinus canicula* (Linnaeus, 1758).

Ginglymostomatidae – Nurse sharks

?Nebrius ferrugineus (Lesson, 1831)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "19. [SQUALUS] c) KUMAL. Dentibus nullis; pinnis pect. brevibus; cirrhis oris quatuor.".

Type locality: – (Red Sea).

Genus name: *Squalus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *kumal*.

Arabic name (Latinised, FORSSKÅL): Kumal.

Remarks: In his draft, FORSSKÅL listed this species as an unidentified *Squalus* with the local name 'kumal', but did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS used the Arabic name as a species name and added a diagnosis. The name would therefore be available as *Squalus kumal* Fabricius [ex Forsskål] in Niebuhr, 1775; it was considered as valid by BONNATERRE (1788: 13). Unfortunately, *Squalus kumal* is most probably a senior synonym of the commonly used name *Nebrius ferrugineus* (Lesson, 1831). The species was considered as valid by WALBAUM (1792: 523). As the name *Squalus kumal* has not been used otherwise, it is rejected in accordance with Art. 23.2 and the preamble of ICZN; an application to the International Commission on Zoological Nomenclature will be needed to retain the name *Scyllium ferrugineum* Lesson, 1831 for this species, which is considered to be valid, with the currently used name *Nebrius ferrugineus* (Lesson, 1831). The species was subsequently named *Squalus kamul* by BLOCH & SCHNEIDER (1801: 138, under 'species non determinandae'), which is not an independent species description, but a spelling error for *Squalus kumal*.

Lamnidae – Mackerel sharks

Carcharodon carcharias (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SQUALUS] *lamia*.".

Locality: "Melita" (La Valletta/Malta). Maltese name: "Il gabdol".

Remarks: This is a name only (nomen nudum), listed as *Squalus lamia* Forsskål in Niebuhr, 1775; this name is not available, as it was neither accompanied by a diagnosis nor a description. From the name 'lamia', which is the local Italian name for *Carcharodon carcharias*, it can be concluded that this record may have been based on *Carcharodon carcharias* (Linnaeus, 1758). The species was subsequently described as *Carcharias lamia* Rafinesque-Schmaltz, 1810 (RAFINESQUE-SCHMALTZ 1810: 44), which is a junior synonym of *Carcharodon carcharias* as well. This species, however, may have been confused with the basking shark *Cetorhinus maximus* (Gunnerus, 1765), which has the actual Maltese vernacular name 'Gabdoll' (Anonymus 2007b).

Triakidae – Hound sharks

?Mustelus sp.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "20. [SQUALUS] d) KELB EL BAHR: i. e. *canis marinus*.".

Type locality: – (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Genus name: *Squalus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *kelb el bahr*.

Arabic name (Latinised, FORSSKÅL): Kelb el bahr.

Remarks: In his draft, FORSSKÅL treated this as a species of *Squalus* which was called 'Kelb el Bahr', but was considered identical with *Canis marinus* (or *Squalus canis marinus*?). He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS used '*kelb el bahr*' as species name, but *Squalus kelb el bahr* Fabricius [ex Forsskål] in Niebuhr, 1775 is not available because the species name is not binominal (ICZN, Art. 5), because the name is not accompanied by a diagnosis or by distinguishing characters, and because it is described in synonymy.

Mustelus sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[PETROMYZON] *mustela*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Mustilla".

Remarks: The species name '*mustela*' was erroneously listed under *Petromyzon lampetra*. This was obviously an error by FABRICIUS in NIEBUHR (1775a), who confused the two species and switched lines. As the name '*mustela*' is just a listing of the name, the record cannot be confirmed and assigned to species level; it could have been based on either *Mustelus asterias* Cloquet, 1821, *Mustelus mustelus* (Linnaeus, 1758), or *Mustelus punctulatus* Risso, 1827.

Carcharhinidae – Requiem sharks

Carcharhinidae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "17. SQUALUS a) MASSASA, *Djiddæ*; MAFREKA, *Lohajæ*. Dentibus nullis; pinnis pect. longis. A Charcharia diversus.".

Type localities: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Genus name: *Squalus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *massasa* or *mafreka*.

Arabic names (Latinised, FORSSKÅL): Massasa, Mafreka; (FABRICIUS in NIEBUHR): Masâsa (wrongly placed, on p. 20 under *Squalus carcharias major*).

Remarks: In his draft, FORSSKÅL clearly treated this as an unidentified species of *Squalus* which was called 'Massasa' at Jeddah and 'Mafreka' at Lohaja. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. ESCHMEYER (2007) also mentions a quotation by FORSSKÅL in NIEBUHR (1775: 20); the name 'Massasa' stated there in a description of *Squalus carcharias*, however, does not refer to this taxon. FABRICIUS in NIEBUHR used both Arabic names as species names, but it is clear from the context that he meant local names as well. Though accompanied by a diagnosis, two alternative species names are given by FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a), *Squalus massasa* or *mafreka*, which means that the name(s) is/are not available. It was, however, subsequently made available as *Squalus messasa* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 13). The species was considered as valid by WALBAUM (1792: 522). This name should be suppressed by the International Commission on Zoological Nomenclature.

Carcharhinidae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIV): "*Squali* [*Squalus*] *carebar*." (in listing of *Echeneis neucrates*, see Echeneidae).

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Squalus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *carebar*.

Arabic name (Latinised, FORSSKÅL): Carebar.

Remarks: This species name is found in the listing of *Echeneis neucrates* (*naucrates*) as its host; no diagnosis is given, so the name is a numen nudum and not available. The author is FABRICIUS [ex FORSSKÅL] in NIEBUHR; the correct name would be *Squalus carebar* Fabricius [ex Forsskål] in Niebuhr, 1775. It was not included in ESCHMEYER (2007). The species is unidentifiable within the family Carcharhinidae.

Carcharhinus melanopterus (Quoy & Gaimard, 1824)

FORSSKÅL in NIEBUHR (1775a: VIII): "19. SQUALUS CARCHARIAS. *Gersch*. [..., Arabic name]. α.) MINOR. *Alka* vel *Æas*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 20): "19. SQUALUS CARCHARIAS. (Arab. *Gersch* vel *Kersch* [..., Arabic name]. OBS. *Djiddæ* duæ Species simillimæ; his tantum notis invicem distinguendæ). *Minor: dentibus* microscopio inspectis, ..." [see also below under *Negaprion acutidens*].

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Squalus*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *carcharias minor*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Alka, Aeas.

Remarks: FORSSKÅL in NIEBUHR (1775a: 20) stated under the heading of *Squalus carcharias*, that at Jeddah two similar species occur, namely *minor* and *major*. The procedure of describing a new species under the heading of another is unusual; on p. VIII, he treats the two as varieties, but on p. 20 explicitly as separate species. Both of them are accompanied by diagnoses and valid available taxa of the species group; I here regard the two as subspecies. In the case of *minor*, the available name is *Squalus carcharias minor* Forsskål in Niebuhr, 1775. The species was considered as valid as *Squalus (Carcharias) minor* by WALBAUM (1792: 514). This is an unused senior synonym of *Carcharias melanopterus* Quoy & Gaimard, 1824, with the frequently used common name *Carcharhinus melanopterus*. According to ICZN, the unused older name can be disregarded. In order to stabilise the current usage of the species name, a petition to the International Commission on Zoological Nomenclature is needed to suppress the name *Squalus carcharias minor*.

Negaprion acutidens (Rüppell, 1837)

FORSSKÅL in NIEBUHR (1775a: VIII): "19. SQUALUS CARCHARIAS. *Gersch*. [..., Arabic name]. β) MAJOR. *Zyfa*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 20): "19. SQUALUS CARCHARIAS. Arab. *Gersch* vel *Kersch* [..., Arabic name]. OBS. *Djiddæ* duæ Species simillimæ; his tantum notis invicem distinguendæ. *Major: pinnis dors.* immaculatis, ...".

Type localities: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Genus name: *Squalus*.
Species/subspecies name (Forsskål, Fabricius in Niebuhr): *carcharias major*.
Arabic names (Latinised, Forsskål): Zyfa, Aeas (Lohaja), Jecore, Sife; (Fabricius in Niebuhr): Aka, Aeas.
Remarks: Forsskål in Niebuhr (1775a: 20) stated under the heading of *Squalus carcharias*, that at Jeddah two similar species occur, namely *minor* and *major*. The procedure of describing a new species under the heading of another is unusual; on p. VIII, he treats the two as varieties, but on p. 20 explicitly as separate species. Both of them are accompanied by diagnoses and are available taxa; I here regard the two as subspecies. In the case of *major*, the available name is *Squalus carcharias major* Forsskål in Niebuhr, 1775. It was subsequently mentioned as *Squalus (Carcharias) major* by Walbaum (1792: 514); this is not an independent subspecies/variety description as assumed by Eschmeyer (2007). *Squalus carcharias major* Forsskål in Niebuhr, 1775 is apparently an unused senior synonym of *Carcharias acutidens* Rüppell, 1837 (Rüppell 1837: 65, pl. 18, fig. 3), with the frequently used name *Negaprion acutidens* (Rüppell, 1837). To retain the latter name, and suppress its unused senior synonym, will require a petition to the International Commission on Zoological Nomenclature.

Sphyrnidae – Hammerhead sharks

Sphyrna sp.

Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Squalus] *zygaena*.".
Locality: "Melita" (La Valletta/Malta). Local name: "Il Marsel".
Remarks: This is a name only in a list, and not assignable to species; the record could have been based on either *Sphyrna tudes* (Valenciennes, 1822) or *Sphyrna zygaena* (Linnaeus, 1758).

Sphyrna mokarran (Rüppell, 1837)

Forsskål in Niebuhr (1775a: X): "21. [SQUALUS] e) zygaena, *Kornae* [..., Arabic name] vel *Mokarran. Mascatensibus* vocatur *Abu kott*. ...".
Locality: – (Red Sea); "*Mascat*" (Muscat/Oman, 23°37'N 58°35'E). "Rarum ad littora Arabiae.".
Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Kornae, Mokarran, Abu kott.
Remarks: This is a misidentification of *Sphyrna zygaena* (non Linnaeus, 1758). The locality 'Mascat' and Muscatese local name was evidently added by Niebuhr, as Forsskål never visited that city. This species was later described as *Zygaena mokarran* by Rüppell (1837: 66–67, pl. 17, fig. 3).

Oxynotidae – Rough sharks

Oxynotus centrina (Linnaeus, 1758)

Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Squalus] *centrina*.".
Locality: "Melita" (La Valletta/Malta).

Dalatiidae – Kitefin sharks

Etmopterus spinax (Linnaeus, 1758)

Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Squalus] *spinax*.".
Locality: "Melita" (La Valletta/Malta). Local Maltese names: "Il Chelp", "Il Babar".
Remarks: A note by Fabricius [ex Anonymus, Forsskål] in Niebuhr (1775a: XVIII) states that this species is identical with the species named by the Arabs 'Kelb el Bahr'. However, Fabricius [ex Forsskål] in Niebuhr (1775a: X) states that 'Kelb el Bahr' is identical with *Squalus canis marinus*, which is *Galeorhinus galeus* (Linnaeus, 1758). Apparently, Fabricius [ex Forsskål] in Niebuhr (1775a: XVIII) missed a species name here, and added the comment on 'Kelb el Bahr' to the wrong species name.

Squatinidae – Angel sharks

Squatina sp.

Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Squalus] *squatina*.".
Locality: "Melita" (La Valletta/Malta).
Remarks: This is a record of the Linnaean species *Squalus squatina*; it cannot be assigned to species level, as it could have been based on either *Squatina aculeata* Cuvier [ex Duméril], 1829, *Squatina oculata* Bonaparte, 1840, or *Squatina squatina* (Linnaeus, 1758).

Torpedinidae – Torpedo electric rays

Torpedo torpedo (Linnaeus, 1758)

Forsskål in Niebuhr (1775a: IX): "11. RAJA: a) torpedo? Μεδιάςρα. In. *Archipelago*.".
Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Raja] *torpedo*.".
Localities: "In archipelago" (Greek or Turkish islands in the Aegean Sea); "Melita" (La Valletta/Malta).
Remarks: This record is based on *Torpedo torpedo* (Linnaeus, 1758); the other references by Forsskål in Niebuhr (1775: VIII, 15–16) are based on a misidentification of *Malapterurus electricus*. The name *Torpedo* of Forsskål in Niebuhr (1775a) cannot be considered as a new genus description, but is linked as a species name to the genus *Raja*. The first available description of the generic name *Torpedo* is by Duméril (1806).

Pristidae – Sawfishes

Pristis sp.

Fabricius [ex Forsskål] in Niebuhr (1775a: X): "18. [SQUALUS] b) pristis. Abu minschar, [..., Arabic name]. *Djiddæ*. Schækra, *Lohajæ*.".
Localities: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia); "*Lohajæ*" (Al-Luhayya/Yemen).
Genus name: *Squalus*.
Species/subspecies names (Forsskål): *pristis*; (Fabricius in Niebuhr): *pristis abu minschar* or *pristis schaekra*.
Arabic names (Latinised, Forsskål): Abu Minschar, Schaekra.
Remarks: In his draft, Forsskål listed this species as *Squalus pristis* Linnaeus, 1758, together with two local Arabic names. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr used the Arabic name like subspecies names; however, as *abu minschar* is consisting of two words, it cannot be considered as an available subspecies name. Also, both species/subspecies names *Squalus pristis abu minschar* Fabricius [ex Forsskål] in Nie-

buhr, 1775 and *Squalus pristis schaekra* Fabricius [ex Forsskål] in Niebuhr, 1775 are given without a diagnosis and are therefore invalid. Both are referable to either *Pristis pectinata* Latham, 1794 or *Pristis zijsron* Bleeker, 1851.

Pristis pristis (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "SQUALUS *pristis*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il Sia".

Remarks: The actual vernacular Maltese name is "Sija" (Anonymus 2007b).

Rhinobatidae – Guitarfishes

"*Glaucostegus halavi* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: VIII): "18. [RAJA] e) HALAVI: [..., Arabic name] rhinobates.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 19–20): "18. RAJA HALAVI. Arab. [..., Arabic name]".

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *halavi*.

Arabic name (Latinised, FORSSKÅL): Halavi.

Remarks: In his draft, FORSSKÅL treated this species as *Raja* sp. with the Arabic name 'halavi'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR confused species name and Arabic name and used the latter as species name. The name is not binominal in FORSSKÅL's version, but binominal in FABRICIUS in NIEBUHR's version. Therefore, the authorship would be attributed to FABRICIUS [ex FORSSKÅL] in NIEBUHR. The name is accompanied by a diagnosis and description, and would be available as *Raja halavi* Fabricius [ex Forsskål] in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 5) and WALBAUM (1792: 535); the actual name would be *Glaucostegus halavi* (Fabricius [ex Forsskål] in Niebuhr, 1775) (see also ESCHMEYER 2007), with the authorship pending a decision of ICZN.

Rhynchobatus djiddensis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: VIII): "17. [RAJA] d) DJIDDENSIS: maxima. *Rgèt*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 18–19): "17. RAJA DJIDDENSIS; *caudæ pinna biloba; oculeorum ordine initio dorsi triplici, dein simplici; pinna dorsi prima supra pinnas ventrales*.".

Type localities: "*Djiddæ* in Mari rubro" (Jeddah, Juddah/Saudi Arabia); "Perhibetur, illam alia non frequentare littora quam Arabiae Hedsjâs; haud vero ad *Sués*" (Suez, As-Suways/Egypt) "vel *Móchham*" (Al-Mukhā/Yemen) "videri; quod vix crediderim, quum mihi *Lohajæ*" (Al-Luhayya/Yemen) "obveniebat.".

Genus name: *Raja*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *djiddensis*.

Arabic names (Latinised, FORSSKÅL): Rgèt; (FABRICIUS in NIEBUHR): Rget, Bokhát (Lohaja), Aerâb.

Remarks: This species was described binominally with a valid scientific species name by FORSSKÅL, with no change by FABRICIUS in NIEBUHR, so the author is FORSSKÅL in NIEBUHR, and the name is available. It is available as *Raja djiddensis* Forsskål in Niebuhr, 1775 (treated as a valid species since BONNATERRE 1788: 5 and WALBAUM 1792: 534–535). BLOCH & SCHNEIDER (1801: 356) misspelled the name as *Rhinobatus djidensis*, and RÜPPELL (1829: 54–55) as *Rhinobatus djeddensis*.

Rajidae – Skates

Rajidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[RAJA] *mus marinus*. (piscis novus).".

Locality: "Melita" (La Valletta/Malta).

Remarks: This new species name is not binominal (ICZN, Art. 5), and a nomen nudum, as it is neither accompanied by a diagnosis, nor a description or an indication; the name cannot be assigned to a species, and is not available.

Dipturus batis (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[RAJA] *batis*.".

Locality: "Melita" (La Valletta/Malta).

Dasyatidae – Whiptail stingrays

Dasyatidae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: IX): "15. [RAJA] e) SCHOUKIE *Djiddæ*. Aculeis remotiusculis. E pelle hujus Rajae conficiuntur in urbe *Suaken* Vaginæ gladiorum.".

Type localities: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia); "*Suaken*" (Sawākin/Sudan, 19°07'N 37°20'E).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *schoukie*.

Arabic name (Latinised, FORSSKÅL): Schoukie.

Remarks: FORSSKÅL treated this species as an unidentified species of *Raja* with the Arabic name 'Schoukie'; NIEBUHR, however, used the Arabic name as a species name. The name is binominal, accompanied by a diagnosis, and therefore would be available as *Raja schoukie* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN. It was considered as valid by WALBAUM (1792: 536), and misspelled as *Raja schoukia* by BONNATERRE (1788: 6). The record from Suaken (Sawakin/Sudan) is not based on a specimen, but on an information either FORSSKÅL or NIEBUHR probably received in Jeddah. This species is listed as *Raja schoukie* by BLOCH & SCHNEIDER (1801: 368–369) under 'species non determinandae' (undetermined species).

Dasyatis sp.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: IX): "13. [RAJA] c) ARNAK *Lohajæ*. Dentibus granulatis; corpore orbiculato, argenteo; cauda tereti; apterygia, spinis duabus.".

Type locality: "Lohajæ" (Al-Luhayya/Yemen).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *arnak*.

Arabic name (Latinised, FORSSKÅL): Arnak.

Remarks: This is not a misspelling for 'uarnak', but a separate species, as noted by FABRICIUS in NIEBUHR (1775a: IX) in the diagnosis of *Raja omm es scherit*. In his draft, FORSSKÅL treated this species as an unidentified species of *Raja* with the Arabic name 'Arnak'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS, however, used the Arabic name as a species name. The name is binominal, accompanied by a diagnosis and would therefore be available as *Raja arnak* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of

ICZN. The species was treated as valid by WALBAUM (1792: 536) and BLOCH & SCHNEIDER (1801: 364–365). It is not identifiable within the genus *Dasyatis*.

Dasyatis pastinaca (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[RAJA] *pastinaca*.".

Locality: "Melita" (La Valletta/Malta).

Himantura uarnak (Gmelin [ex Forsskål], 1789)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: VIII): "16. [RAJA] c) SEPHEN: [..., Arabic name] β *Uarnak*; [..., Arabic name] cauda apterygia.".

FORSSKÅL in NIEBUHR (1775a: 18): "16. b.) RAJA. Arab. *Uárnak*, [..., Arabic name] similis descriptæ [*Raja sephen*], sed tota maculata, spina una vel duplici in cauda, quæ apterygia.".

GMELIN [ex FORSSKÅL] (1789: 1509–1510): "(RAJA) Uárnak. γ) Raja tota maculata. *Forsk*. Fn. arab. p. 18. ...".

Type locality: – (Red Sea).

Genus name: *Raja*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): –.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Uárnak.

Remarks: In his draft, FORSSKÅL treated this species as a variety of the *Raja* sp. with the Arabic name 'sephen', but with a different local name 'uárnak'. FABRICIUS in NIEBUHR did the same and noted 'Uárnak' as the local Arabic name; the name *arnak* he used in one version is a separate species (see above). The name is neither available from FORSSKÅL's nor from FABRICIUS in NIEBUHR's versions (indicated by italics and is clearly intended to be a local Arabic name rather than a species name, in the version on p. 18 even indicated with 'Arab.' as Arabic name). Therefore, the authorship of the name rests with FORSSKÅL in NIEBUHR (no change in interpretation from FORSSKÅL to FABRICIUS in NIEBUHR), but the name is not available as no scientific species name was given except *Raja sephen* and a local Arabic name. The first author using the name *Raja uarnak* in a correct binominal way was GMELIN [ex FORSSKÅL] (1789: 1509–1510), who is therefore the valid author of the species name. A previous author, BONNATERRE (1788: 4) only named this species as "L'Uarnak", without proposing a scientific name. The currently used name of the species is *Himantura uarnak* (Gmelin [ex Forsskål], 1789). The species was subsequently mentioned as *Raja Uàrnak* (spelled *Raja uarnata* in the index on p. 713) by WALBAUM (1792: 534, 713); the latter is not an independent species description, but a spelling error.

Himantura uarnak (Gmelin [ex Forsskål], 1789)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: IX): "12. [RAJA] b) OMM ES SCHERIT: [..., Arabic name] Cauda tereti, maculata: Piscis simillimus Rajis Uarnak & Arnak.".

Type locality: – (Red Sea).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *omm es scherit*.

Arabic name (Latinised, FORSSKÅL): Omm es scherit.

Remarks: In his draft, FORSSKÅL treated this species as an unidentified species of *Raja* with the Arabic name 'omm es scherit'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR, however, used the Arabic name as species name. As the species name is made up of three words, the name is not binominal and thus not available (ICZN, Art. 5). ESCHMEYER (2007) treated this species as available and used the combined name *Raja ommescherit*, within the family Dasyatidae. This species was subsequently described as *Raja Scherit* by BONNATERRE [ex FORSSKÅL] (1788: 6), which is available; as this name is a junior synonym of and would threaten the frequently used name *Himantura uarnak* (Gmelin [ex Forsskål], 1789), a petition to the International Commission on Zoological Nomenclature will be necessary to suppress the unused name *Raja scherit* Bonnaterre [ex Forsskål], 1788. – This species was mentioned with the new name *Raja ommescherit* by BLOCH & SCHNEIDER (1801: 368); this, however, cannot be considered as a species description, as BLOCH & SCHNEIDER listed it under 'species non determinandae'.

"*Pastinachus sephen* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: VIII): "16. [RAJA] c) SEPHEN: [..., Arabic name] α) pterouros, aculeis caudæ serratis.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 17–18): "16. RAJA SEPHEN; *corpore suborbiculato; cauda duplo longiore subtus alata, supra aculeis duobus longis, utrinque serratis*.".

Type locality: "*Djiddæ* in Mari rubro" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *sephen*.

Arabic names (Latinised, FABRICIUS in NIEBUHR): Saefaen, Syfen, Sif.

Remarks: In his draft, FORSSKÅL treated this species as *Raja* sp. with the Arabic name 'sephen'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR confused scientific and Arabic names and used the latter as species name. The name is not binominal in FORSSKÅL's version, but binominal in FABRICIUS in NIEBUHR's version (who changed the Arabic name from 'Saephaen' or 'Syfen' to *sephen*). Therefore, the authorship would be attributed to FABRICIUS [ex FORSSKÅL] in NIEBUHR. The name would be available as *Raja sephen* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN. The species was treated as valid since WALBAUM (1792: 533–534). This species was re-named *Trigon forskalii* Rüppell, 1829 (RÜPPELL 1829: 53, pl. 13, fig. 2), which is a junior synonym of *Raja sephen*.

"*Taeniura lymma* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: VIII): "15. [RAJA] b) LYMMA. [..., Arabic name] caeruleo-maculata.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 17): "15. RAJA LYMMA. Arab. [..., Arabic name] *Corpore ovali, testaceo, maculis cæruleis; cauda pinnata aculeo uno*.".

Type locality: "Ad urbem *Lohajam* in Mari rubro" (Al-Luhayya/Yemen).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *lymma*.

Arabic name (Latinised, FORSSKÅL): Lymma.

Remarks: In his draft, FORSSKÅL treated this species as *Raja* sp. with the Arabic name 'lymma'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR confused scientific and Arabic names and used the latter as species name. The name is not binominal in FORSSKÅL's version, but binominal in FABRICIUS in NIEBUHR's version. Therefore, the authorship would be attributed to FABRICIUS [ex FORSSKÅL] in NIEBUHR. The name would be available as *Raja lymma* Fabricius [ex Forsskål] in Niebuhr,

1775, with the authorship pending a decision of ICZN. It was treated as valid since WALBAUM (1792: 533), but misspelled *Raja lymnia* by BONNATERRE (1788: 5), and *Raja lymna* by BLOCH & SCHNEIDER (1801: 365).

Gymnuridae – Butterfly rays

Gymnura altavela (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "RAJA *altavela*.".

Locality: "Melita" (La Valletta/Malta).

Myliobatidae – Eagle rays

Aetobatis narinari (Euphrasen, 1790)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: IX): "16. [RAJA] f) MULA [..., Arabic name] pelagica. *Djiddæ*, rarior. Cauda tereti, variegata: ventre niveo: aculeo caudæ admodum nocivo. Nocturno tempore propius ad littora venit.".

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Raja*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *mula*.

Arabic name (Latinised, FORSSKÅL): Mula.

Remarks: In his draft, FORSSKÅL treated this species as an unidentified species of *Raja* with the Arabic name 'Mula', and did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR, however, used the Arabic name as a species name. The name is binominal, accompanied by a diagnosis and therefore would be available as *Raja mula* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN; the species was treated as valid by BONNATERRE (1788: 6) and WALBAUM (1792: 536). *Raja mula* is an unused senior synonym of *Raja narinari* Euphrasen, 1790. The name *Raja mula* is rejected, in accordance with Art. 23.2 and the preamble of ICZN; an application to the International Commission on Zoological Nomenclature will be necessary to retain the name *Raja narinari*, which is considered as a valid species, with the currently used name *Aetobatis narinari* (Euphrasen, 1790).

Aetobatis narinari (Euphrasen, 1790)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: IX): "14. [RAJA] d) TAJARA. [..., Arabic name] Djiddæ. HÖRRÆKA: Lohajæ. Cauda tereti; ventre niveo. Capta, vehementer pinnis verberat.".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Genus name: *Raja*.

Species names (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *tajara* or *hoerraeka*.

Arabic names (Latinised, FORSSKÅL): Tajara, Hörraeka.

Remarks: In his draft, FORSSKÅL treated this species as an unidentified species of *Raja* with two different Arabic names, 'Tajara' at Jeddah and 'Hörraeka' at Al-Luhayya. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR, however, used the Arabic names as two alternative species names, but had only a single diagnosis for them; he did not decide which of the two names to choose as species name. Therefore, we are left with a species name *Raja tajara hoerraeka*, which is not binominal and therefore not available (ICZN, Art. 5). The species was subsequently described as *Raja Tajara* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 6; treated as valid by WALBAUM 1792: 536), which is available, and a senior synonym of *Raja narinari* Euphrasen, 1790. The species is named *Aetobatis narinari* (Euphrasen, 1790) under current usage. To preserve the stability of nomenclature, it will be necessary to petition the International Commission on Zoological Nomenclature to suppress the name *Raja tajara* Bonnaterre [ex Forsskål], 1788.

Myliobatis aquila (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[RAJA] *aquila*.".

Locality: "Melita" (La Valletta/Malta).

Acipenseridae – Sturgeons

Acipenser sturio Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "ACIPENSER *sturio*.".

Locality: "Melita" (La Valletta/Malta).

Huso huso (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[ACIPENSER] *huso*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a very interesting record of the species from Malta. From records in the early 20th century, the species was known to be endemic to the Caspian Sea, Black Sea and Aegean Sea and adjacent watersheds. Though the species spawns in fresh water habitats which are not available in Malta, adults of the Aegean Sea population would have been capable of dispersing through the Mediterranean Sea towards Malta. The species may have been more widespread around the eastern Mediterranean in the past. Today, it is critically endangered in Turkish Black Sea (FRICKE et al. 2007: 22), and extinct in the Aegean Sea (and the Mediterranean).

Actinopterygii – Ray-finned fishes

Actinopterygii, incertae sedis

FORSSKÅL in NIEBUHR (1775a: XIII): "105. [CYPRINUS] c) LEUCISCUS: *Abu grymbi*.".

FORSSKÅL in NIEBUHR (1775a: 71): "105. CYPRINUS LEUCISCUS; (LINN.) *cauda subæquali, P. D. & A. ovatis*. ...".

Material: ZMUC P.261686 (1 dry skin).

Localities: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); "LOHAJÆ" (Al-Luhayya/Yemen).

Remarks: This is a misidentification of *Cyprinus leuciscus* (non Linnaeus, 1758) [currently used name *Leuciscus leuciscus* (Linnaeus, 1758)], a species restricted to temperate freshwater habitats of Europe and western Asia; the record is unplaceable within the Actinopterygii. – FORSSKÅL in NIEBUHR (1775a: 71) described two varieties of this species; they were, however, not named, except for 'unus' (the one) and 'alter' (the other). *Cyprinus leuciscus unus* and *Cyprinus leuciscus alter* (as listed by ESCHMEYER 2007) cannot be regarded as species names.

Actinopterygii, incertae sedis

FORSSKÅL in NIEBUHR (1775a: XVII): "56. DAREDJ ET TIN [..., Arabic name] (obscurus) Est Hebræorum תחץ".

Locality: – (Red Sea).

Remarks: This is an Arabic and a Hebrew name without a genus,

a diagnosis or description. The name is therefore not available as scientific name; it cannot be placed within the Actinopterygii.

Actinopterygii, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "ESOX *lucius*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Esox lucius* (non Linnaeus, 1758), a species restricted to temperate freshwater habitats of the northern hemisphere; the record is unplaceable within the Actinopterygii.

Actinopterygii, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "OSMERUS *eperlanus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Salmo eperlanus* (non Linnaeus, 1758), now named *Osmerus eperlanus*, a species restricted to the northeastern Atlantic, not occurring south of the Gironde estuary, western France; the record is unplaceable within the Actinopterygii.

M o r m y r i d a e – Elephantfishes

"*Mormyrus kannume* Forsskål in Niebuhr, 1775"

FORSSKÅL in NIEBUHR (1775a: XIII): "111. MORMYRUS KANNUME; [..., Arabic name] rostro prominente.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 74–75): "111. MORMYRUS KANNUME; *rostro decurvo, prominente: pinna D. lineari, longitudine corporis dimidii*.".

Type locality: "DAMIATAE" (Dumyāt/Egypt).

Genus name: *Mormyrus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *kannume*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Kannûme.

Remarks: In his draft, FORSSKÅL used the Arabic name 'kannume' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Mormyrus kannume* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available and valid as *Mormyrus kannume* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN.

E l o p i d a e – Tenpounders

"*Elops machnata* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "100. [ARGENTINA] b) MACHNATA; ossiculo maxillæ infer. *Machnat*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 68–69): "100. ARGENTINA MACHNATA; *lineari-lanceolata, membr. br. ultra* 30 *radios*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.17153 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 25, pl. 36; MØLLER 2006).

Genus name: *Argentina*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *machnata*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Machnat.

Remarks: In his draft, FORSSKÅL used the Arabic name 'machnat' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Argentina machnata* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Argentina machnata* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Elops machnata* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 178) and WALBAUM (1792: 46–47).

A l b u l i d a e – Bonefishes

Albula glossodonta (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XIII): "99. ARGENTINA a) GLOSSODONTA; lingua tuberculis osseis. *Bönuk* [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 68): "99. ARGENTINA GLOSSODONTA; *lingua basi tuberculis osseis dentata*.".

Type localities: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); "LOHAJÆ" (Al-Luhayya/Yemen).

Type material: Syntype: ZMUC P.17152 (dry skin) (listed as holotype by KLAUSEWITZ & NIELSEN 1965: 25, pl. 36; MØLLER 2006; ESCHMEYER 2007).

Genus name: *Argentina*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *glossodonta*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Bönuk.

Remarks: This species was listed by both FORSSKÅL and FABRICIUS in NIEBUHR in both the index and text as *Argentina glossodonta*. The name is binominal in both versions, accompanied by a diagnosis a description, and is therefore available as *Argentina glossodonta* Forsskål in Niebuhr, 1775. The species is considered as valid since WALBAUM (1792: 45–46, *Argentina glossodonta*). *Argentina bonuk* Lacepède [ex Forsskål], 1803 (LACEPÈDE 1803: 365–366, 368–369) was described as an unneeded replacement name for *Argentina glossodonta* Forsskål in Niebuhr, 1775; it is a junior synonym, though it was erroneously assigned to *Albula vulpes* (Linnaeus, 1758) by authors.

A n g u i l l i d a e – Freshwater eels

Anguilla anguilla (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XIV): "1. MURÆNA a) *anguilla*. Αχέλι. Ar. *Tæjeban* [..., Arabic name]. vel *Hannæsch*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "MURÆNA *anguilla*.".

Localities: – ["*Smirna et Constantinopoli*"] (İzmir/Turkey; İstanbul/Turkey); Alexandria? (Egypt); "Melita" (La Valletta/Malta).

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Taejeban, Hannaesch. Maltese name: "Il Sallura".

Remarks: This is a Linnaean species listed by FORSSKÅL in NIEBUHR (1775a), based on *Muraena anguilla* Linnaeus, 1758. The actual vernacular Maltese name is "Sallura" (Anonymus 2007b).

Muraenidae – Moray eels

Echidna zebra (Ahl, 1789)

FORSSKÅL in NIEBUHR (1775a: XIV, in part): "2. [MURÆNA] b) *ophis*. Lohajæ *Far*, Djiddæ *Uuz*.".

Localities: "Lohajæ" (Al-Luhayya/Yemen); "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Muraena*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *ophis*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Far (Al-Luhayya), Uuz (Jeddah).

Remarks: This is a composite species, misidentified in part as *Muraena ophis* (non Linnaeus, 1758).

Muraena helena Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[MURÆNA] *serpens maculatus*.".

Locality: "Melita" (La Valletta/Malta). Maltese name: "Il murina".

Remarks: This is a name only (nomen nudum), and therefore not available; according to the Maltese name, the record has been based on *Muraena helena* Linnaeus, 1758 (actual Maltese vernacular name "Morina").

Ophichthidae – Snake eels

Echelus myrus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[MURÆNA] *myrus*.".

Locality: "Melita" (La Valletta/Malta).

Ophichthus ophis (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XIV, in part): "2. [MURÆNA] b) *ophis*. Χέλι.".

Localities: – ["*Smirna et Constantinopoli*"] (İzmir/Turkey; İstanbul/Turkey).

Remarks: This is a composite species, based in part on *Muraena ophis* Linnaeus, 1758.

Ophisurus serpens (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[MURÆNA] *serpens marinus*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il serpt al báhar".

Remarks: *Muraena serpens marinus* Forsskål [ex Anonymus] in Niebuhr, 1775 was described as a name only (nomen nudum), without a diagnosis, description or indication. It is therefore not an available name. The name was erroneously spelled *Muraena serpens marinis* by ESCHMEYER (2007). It is considered to be identical with *Ophisurus serpens* (Linnaeus, 1758). The actual vernacular Maltese name is "Serpt il-báhar halqu twil" (Anonymus 2007b).

Muraenesocidae – Pike congers

Muraenesox cinereus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "2. [MURÆNA] b) CINEREA; suspecta. *Sjæga*. [..., Arabic name].".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 22): "2. MURÆNA TOTA CINEREA. Arab. *Sjæga* vel *Schæga* [..., Arabic name]. nomen cummune toti huic generi.".

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.31250 (see KLAUSEWITZ & NIELSEN 1965: 13, pl. 1; MØLLER 2006).

Genus name: *Muraena*.

Species names (FORSSKÅL, FABRICIUS in NIEBUHR): *cinerea* or *tota cinerea*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Sjaega, Schaega.

Remarks: This species was listed by FORSSKÅL in NIEBUHR (1775a: X) as *Muraena cinerea*, and then later (p. 22) described as *Muraena tota cinerea*, which is not binominal, but tied by the species code '2' to p. X which is considered as the correct version and therefore available as *Muraena cinerea* Forsskål in Niebuhr, 1775. This species was subsequently described as *Muraena arabica* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 488) as an unneeded new name for *Muraena cinerea* Forsskål in Niebuhr, 1775; *Muraena arabica* is a junior synonym. The currently used name for the species is *Muraenesox cinereus* (Forsskål in Niebuhr, 1775) in the family Muraenesocidae. – This species was transferred to the genus *Conger* under the name *Conger cinereus* by RÜPPELL (1830: 115–116, pl. 29, fig. 1), which was not intended as an independent species description, but was a misidentification of *Muraena tota cinerea* of FORSSKÅL, as explicitly noted in the synonymy (RÜPPELL 1830: 115). The name *Conger cinereus* Rüppell, 1830 is therefore not available. GÜNTHER (1870: 38) treated the congrid species under the name *Conger marginatus* Valenciennes in Eydoux & Souleyet, 1850, with both FORSSKÅL's *Muraena tota cinerea* and RÜPPELL's *Conger cinereus* as questionable synonyms. The first available version of the name is *Conger cinereus* Klunzinger [ex Rüppell], 1871 described by KLUNZINGER (1871: 607–608), where RÜPPELL's misidentification was treated as valid, with RÜPPELL as the author. This, however, causes serious problems, as *Conger flavipinnatus* Bennett, 1832, *Conger marginatus* Valenciennes in Eydoux & Souleyet, 1850, *Conger altipinnis* Kaup, 1856, and *Conger noordziekii* Bleeker, 1857 would all be senior synonyms. As the name *Conger cinereus* is of prevailing usage, I continue to use this name here, but an application to the International Commission on Zoological Nomenclature will be necessary to conserve this name and suppress the synonyms listed above. The currently used name is *Conger cinereus* Klunzinger [ex Rüppell], 1871, in the family Congridae. – FORSSKÅL in NIEBUHR (1775a: 22) named three varieties from Djiddae, *Muraena tota cinerea alba*, *M. tota cinerea flava*, and *M. tota cinerea rubra*. These are nomina nuda, as neither is accompanied by a diagnosis or indication; the names are not available.

Congridae – Conger eels

Conger conger (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[MURÆNA] *conger*.".

Locality: "Melita" (La Valletta/Malta).

Engraulidae – Anchovies

Engraulis encrasicolus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[CLUPEA] *encrasicolus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Sardella".

Stolephorus indicus (Hasselt, 1823)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XVII): "45. [CLUPEA] e) *Schàleb* [..., Arabic name] quod nomen parum differt a voce *Slavon. Saláka*. Parva, digiti longitudine; ar-

gentea; utrinque vitta laterali fulva; dorso cæruleo. Vivam non vidi; sed deglutitam a Scombro reperi.".
Locality: – (Red Sea).
Material: No FORSSKÅL material extant.
Genus name: *Clupea*.
Species names (FORSSKÅL, FABRICIUS in NIEBUHR): *encrasicolus* or *baelama*?
Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Láaf, Bælama, Sardin.
Remarks: In his draft, FORSSKÅL used the Arabic name 'schàleb' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Clupea schaleb* as a new species. ESCHMEYER (2007) listed the name erroneously as *Clupea schaleh* and gave the locality, also erroneously, as 'Izmir and/or Istanbul, Turkey'. The Arabic name and the diagnosis, however, indicate that the species originated from the Red Sea. The name is binominal, accompanied by a diagnosis, and would be available as *Clupea schaleb* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN. The name is a senior synonym of *Engraulis indicus* Hasselt, 1823, which is named *Stolephorus indicus* (Hasselt, 1823) under current usage. In order to stabilise this frequently used name, a petition to the International Commission on Zoological Nomenclature to suppress the name *Clupea schaleb* will be needed.

Thryssa baelama (Bloch & Schneider [ex Forsskål], 1801)
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "107. [CLUPEA] b) ENCRASICOLUS. *Bælama*.".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 72): "107. CLUPEA BÆLAMA, ENCRASICOLUS? DESCR. *Corpus* lanceolatum, digito longius: dig latum altum: compressum, argenteum: dorso fusco: …".
Locality: – (Red Sea).
Material: No FORSSKÅL material extant.
Genus name: *Clupea*.
Species names (FORSSKÅL, FABRICIUS in NIEBUHR): *encrasicolus* or *baelama*?
Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Láaf, Bælama, Sardin.
Remarks: FORSSKÅL misidentified this species as *Clupea encrasicolus* (non Linnaeus, 1758) in his index, and was undecided in the text whether this was a new species for which he used the substitute name 'bælama', or if it was *C. encrasicolus*. Though FABRICIUS in NIEBUHR (1775a) used the name *Clupea bælama, encrasicolus?* in the text, he did not clearly decide if this was a new species or not. Therefore, the name *Clupea baelama* Fabricius in Niebuhr, 1775 is not available (ICZN, Art. 11.5). GMELIN (1789: 1407) referred to *Clupea Baelama* in the synonymy of *Clupea setirostris*; the name is not available from this description either. WALBAUM (1792: 42) copied FORSSKÅL's description and named the species '*Clupea bælama* an *Encrasicolus*?', which is not available for the same reason as FORSSKÅL's description. The first available version of the name is *Clupea baelama* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 429). The species is valid within the family Engraulidae, with the currently used name *Thryssa baelama* (Bloch & Schneider [ex Forsskål], 1801). The species name was misspelled *Engraulis boelama* by KLUNZINGER (1871: 507). BROUSSONET's (1782: 39–41) description of *Clupea setirostris* was based in part on the description of *Clupea encrasicolus, baelama* by FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a). With the lectotype designation by FRICKE (1999: 78), that species was restricted to the currently named *Thryssa setirostris* (Broussonet, 1782), with Tanna/Vanuatu as the type locality.

Chirocentridae – Wolf herrings

"*Chirocentrus dorab* (Forsskål in Niebuhr, 1775)"
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "108. [CLUPEA] c) DORAB; dentex. *Lysan Dorab*.".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 72–73): "108. CLUPEA DORAB; *pinnis ventralibus minutis, labio superiori dentibus porrectis bicorni; inferiori longiori, dentibus validioribus, erectis*.".
Type localities: "DJIDDAE" (Jeddah, Juddah/Saudi Arabia); "MOCHHAE" (Al-Mukhā/Yemen).
Genus name: *Clupea*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *dorab*.
Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Lysan (Jeddah), Machnat or Dorab (Al-Mukhā).
Remarks: In his draft, FORSSKÅL used the Arabic name 'dorab' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Clupea dorab* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Clupea dorab* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Chirocentrus dorab* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid by BONNATERRE (1788: 187). *Clupea dentex* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 428–429) is a junior synonym of *Clupea dorab*.

Clupeidae – Herrings

Clupeidae, indet.
FORSSKÅL in NIEBUHR (1775a: XVII): "41. CLUPEA a) *harengus*. Αρεγγα.".
Locality: Western Turkey or Greek Aegean islands.
Remarks: This record is based on a misdentification of *Clupea harengus* (non Linnaeus, 1758), a species which is restricted to the northwestern and northeastern Atlantic. FORSSKÅL's material was based on an unidentified clupeid fish species.

Clupeidae, indet.
FORSSKÅL in NIEBUHR (1775a: XVII): "43. [CLUPEA] c) Γώνος.".
Locality: Western Turkey or Greek Aegean islands.
Remarks: This is not a valid species group name, as it was given only in Greek characters. The name is neither accompanied by a indication, diagnosis or description, and is not available. It cannot be placed within the family Clupeidae.

Alosa agone (Scopoli, 1786)
FORSSKÅL in NIEBUHR (1775a: XVII, part): "42. [CLUPEA] b) *alosa*. Σαρδέλλα vel Σαυριδηπόλαμύ. Turc. *Sardella-balük*. Arab. Sıgbboga. Macula nigra pone branchias; pinnæ D. & C. albidæ, apice nigræ.".
FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "CLUPEA *alosa*.".
Locality: "Melita" (La Valletta/Malta).
Remarks: These records are based in part on a name only, in part on a short diagnosis, misidentified as *Clupea alosa* (non Linnaeus, 1758). The diagnosis clearly refers to *Alosa agone*.

Judging from the Turkish name, however, other species were included under the name *Clupea alosa* as well; the name 'Sardalya' refers to species of sardines (FRICKE et al. 2007), i. e. *Sardina pilchardus* (Walbaum, 1792), *Sardinella aurita* (Valenciennes in Cuvier & Valenciennes, 1847) and *Sardinella maderensis* (Lowe, 1838).

Amblygaster sirm (Walbaum [ex Forsskål], 1792)

FORSSKÅL in NIEBUHR (1775a: XVII): "44. [CLUPEA] d) *charact. harengi*; sed minor. Arab. *Sirm*. [..., Arabic name] Maxilla inferiore longiore; corpore tripollicari; macula aurea pone oculos. Rad. B. 8. D. 19. P. 16. V. 8. A. 17. C. 18.".

Locality: – (Red Sea).

Material: No FORSSKÅL material extant.

Remarks: FORSSKÅL in NIEBUHR's (1775a: XVII) note on *Clupea* sp. d is the basis for the description of *Clupea Sirm* by WALBAUM [ex FORSSKÅL] (1792: 38) as a variety of *Clupea harengus*, i. e. *Clupea harengus sirm*, which is now named *Amblygaster sirm* (Walbaum [ex Forsskål], 1792). It is uncertain if the basis of this note was really *A. sirm*, as judging from the colour description it may well have been *Herklotsichthys quadrimaculatus* (Rüppell, 1837). No type material of *Clupea harengus sirm* Walbaum [ex Forsskål], 1792 is known. It would therefore be advisable to describe a neotype for the species.

Chanidae – Milkfishes

"*Chanos chanos* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIV): "110. [MUGIL] b) CHANOS; pinna D. unica. *Anged*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 74): "110. MUGIL CHANOS; *pinna dorsi unica; p. caudæ utrinque bi-alata*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.17154 (1 dry skin) (see KLAUSEWITZ & NIELSEN 1965: 26, pl. 37; MØLLER 2006).

Genus name: *Mugil*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *chanos*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Anged; Turkish name of variety 'b': Chani.

Remarks: In his draft, FORSSKÅL used the Turkish name 'chani' as a substitute for a Latin name possibly to be selected for his variety 'b'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) confused the two varieties, and described *Mugil chanos* as a new species for the variety 'a'. The name is binominal, accompanied by a diagnosis and description, and would be available as *Mugil chanos* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Chanos chanos* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 180–181) and WALBAUM (1792: 227–228). It was subsequently re-named *Chanos arabicus* Lacepède [ex Forsskål], 1803 (LACEPÈDE 1803: 395, 396), which is available, but a junior synonym of *Mugil chanos*. – ESCHMEYER (2007) erroneously gave ZMUC P.17154 as a syntype, and added ZMUC P.17151 as a further syntype. The latter specimen, however, is not a FORSSKÅL specimen, but a *Denticeps clupeoides* Clausen, 1959 from West Africa, collected in 1958, according to the ZMUC database (http://zoologi.snm.ku.dk/samlinger/vertebrates/dokument3/). – The Turkish name 'chani' leads to the suspicion that this may be a composite species, based in part on Turkish Mediterranean material which would belong to a different family. In Turkey, several serranid fish species have the actual name 'hani' (FRICKE et al. 2007). For the sake of the stability of nomenclature, I here treat the species as if exclusively based on the Red Sea syntypes, ignoring possible Mediterranean origins of the name.

Cyprinidae – Minnows and carps

"*Barbus bynni* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "103. CYPRINUS a) BYNNI; niloticus. *Bynni*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 71): "103. CYPRINUS BYNNI; *pinna dorsali radiis* 13; *tertio crasso, corneo*.".

Type locality: "Niloticus" (River Nile/Egypt).

Type material: Neotype: BMNH 1907.12.2.1230 from Nile/Egypt; designation by BANISTER (1973: 27).

Genus name: *Cyprinus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *bynni*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Bynni.

Remarks: In his draft, FORSSKÅL used the Arabic name 'bynni' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Cyprinus bynni* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Cyprinus bynni* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Barbus bynni* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species is considered as valid since WALBAUM (1792: 22–23, *Cyprinus Bynni*). This name was misspelled as *Cyprinus binny* by LACEPÈDE (1803: 490, 530).

Labeo vulgaris Heckel, 1847

FORSSKÅL in NIEBUHR (1775a: XIII): "104. [CYPRINUS] b) NILOTICUS. *Lebes* [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 71): "104. CYPRINUS NILOTICUS. Arab. *Lebés*. [..., Arabic name]".

Locality: "Niloticus" (River Nile/Egypt).

Material: Neotype: BMNH 1907.12.2.1074, as designated by REID (1985: 61); neotype designation invalid, as the species is objectively invalid.

Remarks: This is not an independent new species description, but is based on *Cyprinus niloticus* Linnaeus, 1758. Though this species was incorrectly treated as valid as *Labeo niloticus* (Forsskål, 1775) by LÉVÊQUE & DAGET (1984: 316) and others, that name is invalid. The first subsequent usage of FORSSKÅL's version of the name *Cyprinus niloticus* is by GEOFFROY SAINT-HILAIRE (1809: pl. 9, fig. 2) (description by GEOFFROY SAINT-HILAIRE 1827: 282–286, *Cyprinus niloticus*), but this is neither available as it is indirectly based on the Linnaean species. Other authors directly referred to the Linnaean species *Cyprinus niloticus* (e. g. WALBAUM 1792: 23). *Labeo vulgaris* Heckel, 1847 (HECKEL 1847: 303, pl. 20, fig. 3) is the first available name for this species.

Citharinidae – Citharinids

Distichodus nefasch (Bonnaterre [ex Forsskål], 1788)

FORSSKÅL in NIEBUHR (1775a: XIII): "[97. SALMO] β) *niloticus. Rai*.".

FORSSKÅL in NIEBUHR (1775a: 66): "97. b) SALMO NILOTICUS,

Linn. est Arabum *Rai*: rad. D. 9. adeoque diversissimus ab *Hasselquistii* qui est Ægyptiorum NEFASCH. M. br. ossibus 4. R. D. 23. dorso virescente: dentibus maxillæ infer. majoribus P. C. basi squamata: …".

Type locality: – (Nile/Egypt).

Remarks: This is not an independent species description, but explicitly refers to *Salmo niloticus* (non Linnaeus, 1758) of HASSELQUIST (1762), which is treated by authors as a valid species of characid fishes, with the name *Distichodus niloticus* (Hasselquist, 1762). This name, however, is not attributable to HASSELQUIST (1762) as this is a rejected work [see Anonymus (1914, 1956), MELVILLE & SMITH (1987: 330)]. Furthermore, neither HASSELQUIST's nor FORSSKÅL's version can be considered as an independent new species description, but both are misidentifications of the Linnaean species *Salmo niloticus*. The first available name for this species is *Salmo nefasch* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 169); the obligatory name is therefore *Distichodus nefasch* (Bonnaterre [ex Forsskål], 1788). – The species was subsequently described as *Salmo aegyptius* Gmelin [ex Hasselquist, Forsskål], 1789 (GMELIN 1789: 1386); this is a junior synonym of *Salmo nefasch* Bonnaterre [ex Forsskål], 1788. The species name was erroneously spelled *Salmo aegyptiacus* by WALBAUM (1792: 83).

Alestiidae – African tetras

Hydrocynus forskahlii (Cuvier, 1819)

FORSSKÅL in NIEBUHR (1775a: XIII): "97. SALMO α) *dentex. Roschâl* […, Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 66): "97. SALMO, Arab. ROSCHAL, […, Arabic name] *pinnis albidis: caudæ dimidio inferiore rubro: colore argenteo.* OBS.: Est *Hasselquistii Salmo dentex*; quem *Linn.* ad Cyprinum rejecit: quamvis huc jure referendus. …".

Locality: – (Nile/Egypt).

Remarks: This is not an independent species description, but explicitly refers to and is a misidentification of *Cyprinus dentex* Linnaeus, 1758, which has the currently used name *Alestes dentex* (Linnaeus, 1758). 'Roschâl' is explicitly meant as the local Arabic name, not as a species or subspecies name. *Salmo dentex* Hasselquist, 1762 (HASSELQUIST 1762: 437) [considered by ESCHMEYER 2007 as not available, as published in a rejected work, see Anonymus (1914, 1956), MELVILLE & SMITH (1987: 330)], was not an independent species description, but just a new generic allocation of *Cyprinus dentex* Linnaeus, 1758. The first available name for this species is *Salmo roschal* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 81–82, as *Salmo Roschal*), which is based on FORSSKÅL in NIEBUHR's (1775a) description of *Salmo dentex*. It is a senior synonym of *Hydrocyon forskahlii* Cuvier, 1819 (CUVIER 1819: 354, pl. 28, fig. 1), which is currently named *Hydrocynus forskahlii* (Cuvier, 1819) (see PARENTI in ESCHMEYER 2007). In order to preserve stability of nomenclature, a petition to the International Commission on Zoological Nomenclature will be needed to suppress the name *Salmo roschal* Walbaum [ex Forsskål], 1792.

Mochokidae – Upside-down catfishes

Synodontis clarias (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XVI): "36 [SILURUS] c) *clarias.* Arab. *Schilân.* […, Arabic name]".

Locality: – (Nile/Egypt).

Remarks: This record is based on the Linnaean species *Silurus clarias*, which is valid, with the currently used name *Synodontis clarias* (Linnaeus, 1758). The *Pimelodus clarias* or 'Scheilan' of GEOFFROY SAINT-HILAIRE (1809: pl. 13, figs. 3–4; 1827: 299–300) is not an independent species description, as assumed by ESCHMEYER (2007), but is a misidentification of *Silurus clarias* Linnaeus, 1758 [to which GEOFFROY SAINT-HILAIRE (1827: 299) explicitly referred], which was confused with and based on *Synodontis schall* (Bloch & Schneider, 1801).

Malapteruridae – Electric catfishes

Malapterurus electricus (Gmelin [ex Forsskål], 1789)

FORSSKÅL in NIEBUHR (1775a: VIII): "14. RAJA a) TORPEDO. *Raasch.* […, Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 15–16): "14. RAJA TORPEDO: *pinna dorsali adiposa, corpore nigro maculato, cirrhis oris sex.*".

Locality: "In Nilo inferiori rarius: mihi obveniebat in pago Benha el ásal ad Nilum jacenti" (River Nile, at Banhā/ Egypt, 30°28'N 31°11'E).

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Raasch.

Remarks: This record is based on a misidentification of *Raja torpedo* (non Linnaeus, 1758). The *Torpedo torpedo* (Linnaeus, 1758) of current usage is a marine species that does not enter brackish water. The species was re-named *Silurus electricus* (Gmelin [ex Forsskål], 1789) (GMELIN 1789: 1354); it is now considered as valid as *Malapterurus electricus* (Gmelin [ex Forsskål], 1789).

Plotosidae – Eeltail catfishes

Plotosus lineatus (Thunberg, 1787)

FORSSKÅL in NIEBUHR (1775a: XVI): "36. [SILURUS] d) Arab. *Boa* vel *Buja.* […, Arabic name] Mocchæ.".

Type locality: "*Mochhæ*" (Al-Mukhā/Yemen).

FORSSKÅL material: ZMUC P.28555 (dry skin). No types known (see KLAUSEWITZ & NIELSEN 1965: 24).

Genus name: *Silurus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): –.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Boa, Buja.

Remarks: ESCHMEYER (2007) listed the name of this species as *Silurus arab* Forsskål, 1775, but the first valid description is by BLEEKER [ex FORSSKÅL] (1862: 111) as *Plotosus arab*. 'Arab.', however, is not a species name, but the abbreviation for 'Arabic', indicating that 'Boa' or 'Buja' are the Arabic names. This is clearly intended to be a *Silurus* sp., not a new species description. Therefore, the name *Silurus arab* is not available out of FORSSKÅL in NIEBUHR's (1775a) description, but as *Plotosus arab* Bleeker [ex Forsskål], 1862. FORSSKÅL's record is based on the species *Plotosus lineatus* Thunberg, 1787, and *Plotosus arab* Bleeker [ex Forsskål], 1862 is a junior synonym of that species.

Clariidae – Airbreathing catfishes

Clarias anguillaris (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XVI): "34. [SILURUS] b) *anguillaris.* Arab. *Harmuth.*".

Locality: – (Nile/Egypt).

Remarks: This record is based on the Linnaean species *Silurus anguillaris*, which is valid, with the currently used name *Clarias anguillaris* (Linnaeus, 1758).

Schilbeidae – Schilbeid catfishes

Schilbe mystus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XVI): "33. SILURUS a) *mystus*. Arab. *Schilbæ* [..., Arabic name]".

Locality: – (Nile/Egypt).

Remarks: This record is based on the Linnaean species *Silurus mystus*, which is valid, with the currently used name *Schilbe mystus* (Linnaeus, 1758).

Bagridae – Bagrid catfishes

"*Bagrus bajad* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "95. [SILURUS] b) BAJAD; [..., Arabic name] niloticus.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 66): "95. SILURUS BAJAD; *pinna dorsi postica adiposa; cirrhis* 8.".

Type locality: "In *Nilo*" (River Nile/Egypt).

Genus name: *Silurus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *bajad*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Bajâd.

Remarks: In his draft, FORSSKÅL used the Arabic name 'bajad' or 'bajâd' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Silurus bajad* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Silurus bajad* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Bagrus bajad* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The name was considered as valid since WALBAUM (1792: 569). It was subsequently misspelled *Porcus bayad* by GEOFFROY SAINT-HILAIRE (1809: pl. 15, figs. 1–2; 1827: 303).

"*Bagrus docmak* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "94. SILURUS a) DOCMAK; radio osseo. *Doqmâq*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 65): "94. SILURUS DOCMAK; *pinna dorsali postica adiposa, ani radiis decem, branch.* 2 *cirrhis octo*.".

Type locality: "In *Nilo* inferiori ad Deltam" (Nile Delta/Egypt).

Genus name: *Silurus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *docmak*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Doqmâk.

Remarks: In his draft, FORSSKÅL used the Arabic name 'docmak' or 'doqmâk' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Silurus docmak* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Silurus docmak* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Bagrus docmak* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 572). The name was subsequently misspelled as *Silurus docmac* by BLOCH & SCHNEIDER (1801: 388) and other authors.

Synodontidae – Lizardfishes

Synodus saurus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[OSMERUS] *saurus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is not an independent species name, but based on *Salmo saurus* Linnaeus, 1758; the species was either deliberately or erroneously transferred into the genus *Osmerus*. *Salmo saurus* is considered as valid with the currently used name *Synodus saurus* (Linnaeus, 1758).

Moridae – Deepsea cods

Moridae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "GADUS *asellus varius*." (Local Maltese name: "L'Afnelli").

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GADUS] *asellus virescens*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GADUS] *asellus mollis*. (Local Maltese name: "Il Munckaro").

Locality: "Melita" (La Valletta/Malta).

Remarks: These are names only (nomina nuda); they are neither accompanied by diagnoses nor indications, and are therefore not available.

Merluccidae – Merluccid hakes

Merluccius merluccius (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GADUS] *merluccius*.".

Locality: "Melita" (La Valletta/Malta).

Phycidae – Phycid hakes

Ciliata mustela (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[BLENNIUS] *mustela*.".

Locality: "Melita" (La Valletta/Malta).

Gaidropsarus mediterraneus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XIV, part): "5. GADUS *mediterraneus*. Γάλια. TURC. *Djelindsjik balük*. Pinna D. unica; nam prioris pinnae loco non sunt nisi ramenta tenuia in sulco depresso.".

Localities: "Turc." (probably both İzmir/Turkey, and İstanbul/Turkey), possibly also at Greek Aegean Sea islands.

Turkish name (FORSSKÅL's transcription): Djelindsjik balük. Actual Turkish name: Gelincik balığı (FRICKE et al. 2007: 65).

Remarks: This species was listed by FORSSKÅL in NIEBUHR as *Gadus mediterraneus*, which clearly refers to the Linnaean species of this name. However, FABRICIUS in NIEBUHR apparently switched lines and added the diagnosis of *Gadum* Σαλαρία under this heading, which clearly belongs to a different species, namely *Salaria basilisca* (Valenciennes in Cuvier & Valenciennes, 1836) (family Blenniidae, see below). The identity of the proper *Gadus mediterraneus* is confirmed by its local Turkish name 'Gelincik balığı', which is used for the three species of *Gaidropsarus* occurring in the Sea of Marmara and the Aegean Sea [*G. biscayensis* (Collett, 1890), *G. mediterraneus* (Linnaeus, 1758) and *G. vulgaris* (Cloquet, 1824), see FRICKE et al. (2007: 64–65)]; the species which is most common in inshore water and most likely to be found in fish markets is *Gaidropsarus mediterraneus*.

Gadidae – Cods

Gadidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GADUS] *æglefinus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This species has been misidentified as *Gadus aeglefinus* (non Linnaeus, 1758), a species that does not occur south of the Bay of Biscay. The Maltese record cannot be assigned to a species; it is based on either *Merlangius merlangus* (Linnaeus, 1758), *Trisopterus luscus* (Linnaeus, 1758) or *Trisopterus minutus* (Linnaeus, 1758).

Ophididae – Cusk-eels

Ophidiidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "OPHIDION *gryllus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a name only (nomen nudum), and therefore not available; the record could have been based on either *Ophidion barbatum* Linnaeus, 1758, *Ophidion rochei* Müller, 1845 or *Parophidion vassali* (Risso, 1810).

Ophidiidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GADUS] *barbatus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: The record of the Linnaean species name *Gadus barbatus* from Malta cannot be assigned to species level; the record could have been based on either *Ophidion barbatum* Linnaeus, 1758, *Ophidion rochei* Müller, 1845 or *Parophidion vassali* (Risso, 1810).

?Brotula multibarbata (Temminck & Schlegel, 1846)

FORSSKÅL in NIEBUHR (1775a: XIV): "6. OPHIDION. Arab. *Abu gudda*.".

Locality: – (Red Sea).

Genus name: *Ophidion*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): –.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu gudda.

Remarks: This species was named only to the genus level by FORSSKÅL and FABRICIUS in NIEBUHR (1775a). The record most probably refers to *Brotula multibarbata* (Temminck & Schlegel, 1846), which is regularly found in shallow water in both Saudi Arabia and Yemen.

Lophiidae – Goosefishes

Lophius sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "LOPHIUS *piscatorius*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This record is a name only, and it cannot be assigned to species level; the record could have been based on *Lophius budegassa* Spinola, 1807 or *Lophius piscatorius* Linnaeus, 1758.

Mugilidae – Mullets

Mugilidae, indet.

FORSSKÅL in NIEBUHR (1775a: XVI): "[38. MUGIL *cephalus*] β) *minor*: an varietas? Κεφαλόπέλο. Arab. *Gabbasj*. tempora migrandi observat periodica.".

Type locality: – (?Turkey; Red Sea).

Type material: No types known. Material may be among ZMUC P.71371 or ZMUC P.71374.

Genus name: *Mugil*.

Species/subspecies name (FORSSKÅL): *cephalus minor*?

Remarks: This species was listed by FORSSKÅL in NIEBUHR as *Mugil cephalus minor*; FORSSKÅL was uncertain if this was a variety of *Mugil cephalus*. As the name is neither accompanied by an indication, a diagnosis or a description, it is not available as *Mugil cephalus minor* Forsskål in Niebuhr, 1775. The material was of a composite origin, based on juvenile mugilid specimens observed in the Mediterranean and in the Red Sea. The name cannot be placed within the family Mugilidae.

"*Chelon tade* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIV): "[109. MUGIL a) CRENILABIS] δ) *Tâde*: [..., Arabic name] labio unicarinato.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 74): "109 [MUGIL CRENILABIS] d) *Tâde* [..., Arabic name] vel *Ædda: labio unicarinato. Radiis pinnarum spinosis, rigidis*. ...".

Type locality: – (Red Sea).

Genus name: *Mugil*.

Species/subspecies name (FORSSKÅL): –, unnamed variety of *Mugil crenilabis*; (FABRICIUS in NIEBUHR): *tâde, tâde* or *ædda*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Tâde, Ædda.

Remarks: In his draft, FORSSKÅL used the Arabic name 'tâde' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described the new species in two different versions, as a variety *Mugil crenilabis tâde* in the index on p. XIV, and as *Mugil crenilabis*, variety *tâde or ædda* on p. 74. It is assumed that it is meant to be a variety of *Mugil crenilabis* in both versions; though in the version in the text is not available as FABRICIUS did not decide whether to name the variety '*tâde*' or '*ædda*', it would be available from the index as *Mugil crenilabis tade*. Both versions are linked together by the species code '109d'. The name is accompanied by a diagnosis, and would be available by indication (ICZN, Art. 12.2.2) as *Mugil crenilabis tade* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Chelon tade* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 227, *Mugil Tâde* vel *Aedda*). BLOCH & SCHNEIDER (1801: 116) erroneously named this taxon *Mugil crenilabis täde*. – *Mugil planiceps* Valenciennes in Cuvier & Valenciennes, 1836 was regarded as a junior synonym of this species by HARRISON & SENOU (1999: 2091).

Crenimugil crenilabis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XIV): "109. MUGIL a) CRENILABIS. *Arabi*.".

FORSSKÅL in NIEBUHR (1775a: 73): "109. MUGIL CRENILABIS; *pinna dorsali anteriora radiis* 4. *flexilibus: posteriore inermibus: labiis crenatis; inferiore bicarinato*.".

Type locality: "In Mari Rubro" (Red Sea).

Genus name: *Mugil*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *crenilabis*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Arabi.

Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR described this species as *Mugil crenilabis*; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and is therefore available as *Mugil crenilabis* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 180) and WALBAUM (1792: 226–227).

"*Moolgarda seheli* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIV): "[109. MUGIL a) CRENILABIS] β) *Seheli*: integris labiis.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 73–74): "109 [MUGIL CRENILABIS] b) MUGIL SEHELI; præcedentis forte varietas. P. D. *radii* rigidiores: *Labia* sine crenis & ciliis. …".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen); – (Red Sea).

Type material: Syntype: ?ZMUC P.71373 (dry skin) (listed as holotype by MØLLER 2006 and ESCHMEYER 2007) (see KLAUSEWITZ & NIELSEN 1965: 26, pl. 37; material has been confused with *Mugil tade*).

Genus name: *Mugil*.

Species/subspecies name (FORSSKÅL): –, unnamed variety of *Mugil crenilabis*; (FABRICIUS in NIEBUHR): *seheli*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Sehêli, Hari (Lohaja), Tobâr.

Remarks: In his draft, FORSSKÅL used the Arabic name 'seheli' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described the new species in two different versions, as a variety *Mugil crenilabis seheli* in the index on p. XIV, and as *Mugil crenilabis*, variety *Mugil seheli* on pp. 73–74. It is assumed that it is meant to be a variety of *Mugil crenilabis* in both versions; the name is accompanied by a diagnosis and description, and would be available as *Mugil crenilabis seheli* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Moolgarda seheli* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 227, *Mugil Seheli*).

Mugil cephalus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XVI): "38. MUGIL *cephalus*: Κέφαλος. Turc. *Kefal-balük*. Arab. *Buri*. […, Arabic name] Aliis *Mukschen*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "MUGIL *cephalus*." Local Maltese name: "Il Caplar.".

Localities: – (probably both İzmir/Turkey, and İstanbul/Turkey); "Melita" (La Valletta/Malta); – (?Alexandria/Egypt; ?Red Sea).

Mugil cephalus (Linnaeus, 1758)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIV): "[109. MUGIL a) CRENILABIS] γ) *Öûr*: […, Arabic name] labiis ciliatis.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 74): "109 [MUGIL CRENILABIS] c) ÖUR, […, Arabic name] *labio utroque ciliato; inferiori uni-carinato; oculis pinguedine fere obtectis operculo*, subtus & lateribus, atque pone. Macula P. P. oblonga, obliqua. *Vitta* longitudinalis fusca, evidens.".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.71372 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 26, pl. 36; MØLLER 2006).

Genus name: *Mugil*.

Species/subspecies name (FORSSKÅL): –, unnamed variety of *Mugil crenilabis*; (FABRICIUS in NIEBUHR): *crenilabis öur*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Öûr.

Remarks: In his draft, FORSSKÅL used the Arabic name 'öur' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described this taxon as a variety *Mugil crenilabis öur* in both the index and text. The 'ö' is a substitute for the Latin spelling 'oe'. The name is accompanied by a diagnosis and description, and would be available as *Mugil crenilabis oeur* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN. The species was considered as valid by WALBAUM (1792: 227, *Mugil Oeur*). It is, however, a junior synonym of *Mugil cephalus* Linnaeus, 1758.

A t h e r i n i d a e – Old World silversides

Atherina sp.

FORSSKÅL in NIEBUHR (1775a: XIII): "101. ATHERINA a) HEPSETUS. *Geschgusch*. Constantinopoli vocatur Græcis Αδερίνα. …".

Locality: "Constantinopoli" (İstanbul/Turkey).

Remarks: FORSSKÅL in NIEBUHR's (1775a) *Atherina hepsetus* is of a composite origin. Neither can be considered as an independent species description, but refer to *Atherina hepsetus* Linnaeus, 1758; the Constantinople (İstanbul) material is based on either *Atherina hepsetus* Linnaeus, 1758 or *Atherina boyeri* Risso, 1810, while the Djiddae (Jeddah) material is *Atherinomorus forskalii* (see below).

Atherinomorus forskalii (Rüppell, 1838)

FORSSKÅL in NIEBUHR (1775a: 69–70): "101. ATHERINA HEPSETUS. Quam *Hasselquist* eodem descripsit nomine …".

Locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

FORSSKÅL material: ZMUC P.71370 (ex P.101), 1 specimen [indicated as holotype by ESCHMEYER (2007), though the specimen does not have type status].

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu geschgusch, Abu kesckul, Keschkusch.

Remarks: FORSSKÅL in NIEBUHR's (1775a) *Atherina hepsetus* is of a composite origin. Neither is an independent species description, but based on misidentified *Atherina hepsetus* (non Linnaeus, 1758); FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 69) referred to HASSELQUIST's (1757) description from Egypt, while HASSELQUIST referred to LINNAEUS (1758) [HASSELQUIST (1757) rejected for nomenclatural purposes by the International Commission on Zoological Nomenclature, see Anonymus (1914, 1956) and MELVILLE & SMITH (1987: 330)]. While the Constantinople (İstanbul) record is based on *Atherina* sp. (see above), the Djiddae (Jeddah) material was said to be based on *Atherinomorus lacunosus* (see RANDALL 2005: 78). This species was subsequently described as *Atherina forskalii* Rüppell, 1837 (RÜPPELL 1837: 132–133, pl. 33, fig. 1), based in part on FORSSKÅL in NIEBUHR's description. It was considered as valid by KIMURA et al. (2007).

E x o c o e t i d a e – Flyingfishes

Exocoetidae, indet.

FORSSKÅL in NIEBUHR (1775a: XVI): "39. EXOCOETUS a) *volitans*. Arab. *Djerâd el bâhr*, […, Arabic name] i. e. *Gryllus marinus*. Djiddæ *Gharâra*. Mocchæ *Sabari*. Toto itinere navali vidimus hunc piscem subinde catervatim volantem. Habitat sine dubio in Mari rubro, inde tamen minime sequi-

tur, eum suisse Hebræorum *Selnu*, & ad castra usque Israelitarum volitasse.".

Localities: "Djiddae" (Jeddah, Juddah/Saudi Arabia); "Mocchae" (Al-Mukhā/Yemen).

Remarks: Though this record is based on the Linnaean name *Exocoetus volitans* Linnaeus, 1758, it is probably of a composite nature, based on various exocoetid species occurring in the Red Sea. Goren & Dor (1994: 15) listed eight species of the family occurring in the area; most of them may have been seen during Forsskål's expedition and could be the basis for this record. A species named *Exocoetus gryllus* Klunzinger, 1871 (Klunzinger 1871: 586) is a junior synonym of *Parexocoetus mento* (Valenciennes in Cuvier & Valenciennes, 1847).

Hemiramphidae – Halfbeaks

"*Hemiramphus far* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII): "[98. ESOX marginatus] β) *Far*. [..., Arabic name] Lohajæ.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 67): "98. [ESOX marginatus] b) far; *Lohajæ:* huic simillimus; supra lineam argenteam maculis nigris notatus.".

Type locality: "*Lohajæ*" (Al-Luhayya/Yemen).

Genus name: *Esox*.

Species/subspecies name (Forsskål): –; (Fabricius in Niebuhr): *marginatus far*.

Arabic name (Latinised, Forsskål): Far.

Remarks: In his draft, Forsskål used the Arabic name 'Far' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed subspecies at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr described *Esox far* as a variety of *Esox marginatus*; the name was accompanied by a diagnosis, and would be available as *Esox far* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Hemiramphus far* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. This is a valid species.

Hemiramphus marginatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XIII): "98. ESOX α) marginatus; abdomine marginato. Gambarur. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 67): "98. ESOX marginatus; *pinna dorsali anique oppositis; linea laterali argentea; maxilla inferiori sextuplo longiori*.".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.342523 (dry skin) (see Klausewitz & Nielsen 1965: 25, pl. 35; Møller 2006).

Genus name: *Esox*.

Species name (Forsskål, Fabricius in Niebuhr): *marginatus*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Gambarûr.

Remarks: Both Forsskål and Fabricius in Niebuhr described this species as *Esox marginatus*; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and is therefore available as *Esox marginatus* Forsskål in Niebuhr, 1775. This is a valid species, now named *Hemiramphus marginatus* (Forsskål in Niebuhr, 1775).

?Oxyporhamphus bruuni Parin, Collette & Shcherbachev, 1980

Forsskål in Niebuhr (1775a: XVI): "40. [EXOCOETUS] b) *non volitans*: alius eodem nomine arabico, & huic similis; sed macerrimus, meris quasi ossiculis constans.".

Locality: – (Red Sea).

Remarks: This cannot be regarded as an independent new species description, as Forsskål in Niebuhr (1775a) merely stated that this is 'not *volitans*', but did not give a proper species name. The name is neither binominal, nor sufficiently described or diagnosed, and is therefore not available as *Exocoetus non volitans* Forsskål in Niebuhr, 1775; the record was probably based on the hemiramphid *Oxyporhamphus bruuni* Parin, Collette & Shcherbachev, 1980. The name *Exocoetus non volitans* Forsskål in Niebuhr, 1775 was not included in Eschmeyer (2007).

Belonidae – Needlefishes

Belonidae, indet.

Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "[Esox] *bellone*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a record of *Esox belone* (non Linnaeus, 1761); the spelling of the species name as '*bellone*' is erroneous. The record is based on the name only, and cannot be assigned to species level; it may be attributable to either *Belone acus* Risso, 1827, *Belone svetovidovi* Collette & Parin, 1970 or *Tylosurus imperialis* (Rafinesque-Schmaltz, 1810).

Belone acus Risso, 1827

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII) (part): "[98. ESOX] γ) *belone*; Constantinop. Græcis Βελανίδα. Turc. *Sargan baluk*, i. e. *piscis cornutus*.".

Locality: "Constantinopolis" (İstanbul/Turkey).

Remarks: This is a misidentification of *Esox bellone* (non Linnaeus, 1758) or *Esox belone* (non Linnaeus, 1761) (discussion of taxonomy see below under *Tylosurus choram*), a species now named *Belone belone* (Linnaeus, 1761), and restricted to the northeastern Atlantic. Forsskål's Turkish material is based on *Belone acus* Risso, 1827; this species has the actual Turkish name 'Zargana' (Fricke et al. 2007: 69).

Tylosurus acus (Lacepède, 1803)

Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "[Esox] *acus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Syngnathus acus* (non Linnaeus, 1758), under a different genus *Esox* because the author felt that it was related to the belonids. The name cannot be considered as an independent species description; Lacepède (1803: 325, 327, pl. 1, fig. 3) subsequently named the species *Sphyraena acus*. This name was suppressed by Opinion 900 (Anonymus 1969), but the opinion was widely ignored by the ichthyological community since 1965; it is therefore recommended by Eschmeyer (2007) to retain the name *Tylosurus acus* (Lacepède, 1803) as the valid name of the species.

Tylosurus choram (Rüppell, 1837)

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII) (part): "[98. ESOX] γ) *belone*; Chærman. [..., Arabic name]".

Fabricius [ex Forsskål] in Niebuhr (1775a: 67): "98. [ESOX marginatus] c) Esox belone; *Maris Rubri*; linea laterali juxta abdomen; & pinnis pone excisis. *Rad.* B. 14. D. 22. P. 13. V. 7. A. 21. C. 15. Arab. *Chærman* [..., Arabic name] vel *Choram*.".

Locality: "*Maris Rubri*" (Red Sea).

Remarks: This is not an independent species description, but is a misidentification of *Esox bellone* (non Linnaeus, 1758) or *Esox belone* (non Linnaeus, 1761). *Esox bellone* Linnaeus, 1758 is a nomen dubium in Belonidae according to Collette

& PARIN (1970: 17–18); *Esox belone* Linnaeus, 1761 was placed on Official List in Opinion 225 (Anonymus 1954) as the type species of *Belone* Cuvier, 1816, and is now named *Belone belone* (Linnaeus, 1761), a species which is restricted to the northeastern Atlantic. FORSSKÅL's Red Sea material was based on a species that was subsequently described as *Belone choram* by RÜPPELL (1837: 72).

Holocentridae – Squirrelfishes

Holocentridae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "55. [SCIÆNA] m) ABU SAMF. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 49): "55. SCIÆNA ABU SAMF; [..., Arabic name] cum prioribus [*Sciæna spinifera*] forte eadem: aut tantum varietas. Maxime convenit cum *Murdjan*. *Dentes* incisores, validi, conici: molares obtusi. *Opercula* integra: posteriora uno aculeo: anteriora, nuda. *Dorsum* virens, guttis albis. ...".

Type locality: [Djiddæ] (Jeddah, Juddah/Saudi Arabia).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *abu samf*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu samf.

Remarks: In his draft, FORSSKÅL used the Arabic name 'abu samf' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Sciaena abu samf* as a new species. The name is, however, not binominal, as the species name is consisting of two words; though it was accompanied by a diagnosis, it is not available as *Sciaena abu samf* Fabricius [ex Forsskål] in Niebuhr, 1775 (ICZN, Art. 5). The name is neither available from the *Sciaena abu samf* described by WALBAUM (1792: 310–311), as a copy of FORSSKÅL's description, for the same reasons. *Sciaena abusamf* Lacepède [ex Forsskål], 1802 was subsequently described by LACEPÈDE (1802: 307, 311), and is the first available version of the name as it was binominal and accompanied by a diagnosis. The species is at present unplaceable in the family Holocentridae; judging from the description (white spots in dorsal fin, etc.), it may have been based on either "*Neoniphon sammara* (Forsskål in Niebuhr, 1775)", or on *Sargocentron marisrubri* Randall, Golani & Diamant, 1989.

"*Myripristis murdjan* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "52. SCIÆNA i) MURDJAN; labiis retusis. *Murdjân*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 48): "52. SCIÆNA MURDJAN; labiis retusis. Arab. *Murdjan*. [..., Arabic name]".

Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.4041 (part of dry skin, head missing) (see KLAUSEWITZ & NIELSEN 1965: 19, pl. 15; MØLLER 2006).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *murdjan*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Murdjan.

Remarks: In his draft, FORSSKÅL used the Arabic name 'murdjân' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Sciaena murdjan* as a new species. The name is binominal, accompanied by a diagnosis and description, and would be available as *Sciaena murdjan* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Myripristis murdjan* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 120) and WALBAUM (1792: 316). BLOCH & SCHNEIDER (1801: 86) erroneously spelled the name *Perca murdian*.

"*Neoniphon sammara* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "53. [SCIÆNA] k) SAMMARA; albo-ocellata. *Farer. M'sámmer*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44): "SCIÆNA ... 3) FARER: a) branch. radiis 7. b) radiis 8.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 48–49): "53. SCIÆNA SAMMARA; *dorso rubro-ænea: lateribus argenteis: vittis undique obscurioribus, punctis ocellatis*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.4042 (part of dry skin, head missing) (see KLAUSEWITZ & NIELSEN 1965: 19, pls. 15–16; MØLLER 2006).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *sammara*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Farer, Hömri, Msammer.

Remarks: In his draft, FORSSKÅL used the Arabic name 'sammara' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described *Sciaena sammara* as a new species. The name is binominal in both the index and text, accompanied by a diagnosis and description, and would be available as *Sciaena sammara* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Neoniphon sammara* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 120) and WALBAUM (1792: 316–317). The name was misspelled as *Holocentrus samara* by RÜPPELL (1829: 85) and KLUNZINGER (1870: 720–721). "(*Sciaena*) *farer* Forsskål in Niebuhr, 1775" {would be (*Sciaena*) *farer* Fabricius [ex Forsskål] in Niebuhr, 1775} is another name for this species, out of the version on p. 44 (the name was not mentioned by ESCHMEYER 2007); it is binominal, accompanied by a diagnosis, available, and an unused synonym of "*Sciaena sammara* Forsskål in Niebuhr, 1775". I hereby act as the first reviser of this case to select *Sciaena sammara* as the senior synonym.

Sargocentron rubrum (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "51. [SCIÆNA] h) RUBRA; fronte spinosa. *Atâja*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 48): "51. SCIÆNA RUBRA, ATAJA; Arab. Ataja. [..., Arabic name]".

FORSSKÅL locality: – (Red Sea).

Type locality: Off Customs dock, Port Sudan harbor, Sudan, Red Sea, 3–4 m (as defined by neotype).

Type material: Neotype: BPBM 28183, as selected by RANDALL & HEEMSTRA (1985: 17).

Genus name: *Sciaena*.

Species names (FORSSKÅL): *rubra*; (FABRICIUS in NIEBUHR): *rubra* or *ataja*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Ataja.

Remarks: FORSSKÅL intended to describe this new species as *Sciaena rubra*, as listed in the index on p. XI. FABRICIUS in

NIEBUHR (1775a) erroneously used the name *Sciaena rubra, ataja* for the new species in the text on p. 48. Though the latter version is not binominal and therefore not available (ICZN, Art. 5), both versions are linked together by the species code '51'; the version in the index is binominal, it is accompanied by a diagnosis and description on p. 48, and is therefore available by indication (ICZN, Art. 12.2.2) as *Sciaena rubra* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 120) and WALBAUM (1792: 315–316). *Holacanthus ataja* Lacepède [ex Forsskål], 1802 (LACEPÈDE 1802: 526, 530–531) is an unneeded new name for *Sciaena rubra* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Sargocentron spiniferum (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "54. [SCIÆNA] l) SPINIFERA; capite spinoso. *Gabâja*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 49): "54. SCIÆNA SPINIFERA: *rubra; pinnis dorsalibus connexis: capite spinoso, operculi anterioribus spina longissima*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); – (Red Sea).

Type material: Syntype: ZMUC P.4043 (dry skin) (listed as holotype by MØLLER 2006 and ESCHMEYER 2007) (see KLAUSEWITZ & NIELSEN 1965: 19, pl. 16).

Genus name: *Sciaena*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *spinifera*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Gabâja, Gebaja, Asmud.

Remarks: This new species was described by both FORSSKÅL and FABRICIUS in NIEBUHR (1775a) under the name *Sciaena spinifera*. The name is binominal in both the index and text, it is accompanied by a diagnosis and description, and is available as *Sciaena spinifera* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 120–121) and WALBAUM (1792: 317).

Zeidae – Dories

Zeus faber Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[ZEUS] *faber*.".

Locality: "Melita" (La Valletta/Malta). Local name: "l'Aurata".

Syngnathidae – Pipefishes

Syngnathoides biaculeatus (Bloch, 1785)

FORSSKÅL in NIEBUHR (1775a: XVII): "54. SYNGNATHUS *pelagicus*. Arab. *Abu zummâra*. [..., Arabic name] Corpus heptagonum; cauda trigona.".

Locality: – (Red Sea).

Remarks: This cannot be regarded as an independent new species description, but is a misidentification of the species *Syngnathus pelagicus* (non Linnaeus, 1758). FORSSKÅL's record is based on *Syngnathoides biaculeatus* (Bloch, 1785).

Centriscidae – Shrimpfishes

Centriscus scutatus Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XVII): "53. CENTRISCUS *scutatus*. Arab. *Farras el bâhr* vel *Kesah el bâhr*. Est piscis abdominalis non thoracicus; nam Membr. Br. radiata juxta aperturam branchialem, ut reliqui pisces ejusdem ordinis. *Fistulariæ* proximus est. *Rad*. B. 4. D. 3. 10. P. 11. V. 6. A. 11. C. 9. *Lohajæ*.".

Locality: "*Lohajæ*" (Al-Luhayya/Yemen).

Material: No FORSSKÅL material extant.

Remarks: This is not an independent species description, but a record of the Linnaean species *Centriscus scutatus*.

Macroramphosus scolopax (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XIII): "96. [SILURUS] c) CORNUTUS, rostro recurvo. Gall. *Chardonneres*.".

FORSSKÅL in NIEBUHR (1775a: 66): "96. SILURUS CORNUTUS, *pinnis pect. inermibus; radio pinnæ dorsalis primæ dentato*.".

Type locality: "MASSILIÆ" (Marseille/France).

Genus name: *Silurus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *cornutus*.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Silurus cornutus*; the description was accompanied by a diagnosis and description. The name is available as *Silurus cornutus* Forsskål in Niebuhr, 1775. It is a junior synonym of *Macroramphosus scolopax* (Linnaeus, 1758).

Macroramphosus scolopax (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "BALISTES *scolopax*.".

Locality: "Melita" (La Valletta/Malta).

Scorpaenidae – Scorpionfishes

Helicolenus dactylopterus (Delaroche, 1809)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "SCORPÆNA (sp.).".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "I Cipullazza".

Remarks: According to the Maltese name listed by FORSSKÅL, this record is based on the blackbelly rosefish *Helicolenus dactylopterus* (Delaroche, 1809) (actual vernacular Maltese name "Cipullazza ta l'ghajn"; Anonymus 2007b).

Scorpaenidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "COTTUS *scorpius*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "I Scorfua".

Remarks: This is a misidentification of the species *Cottus scorpius* (non Linnaeus, 1758). The actual vernacular Maltese name "Scorfna" (Anonymus 2007b) refers to several species of *Scorpaena* sp.

Scorpaena porcus Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: X): "7. COTTUS a) MASSILIENSIS, ambiguus. Gall. *Rascasse*.".

FORSSKÅL in NIEBUHR (1775a: 24–25): "7. COTTUS MASSILIENSIS, *capite polyacantho, pinnis dorsalibus coadunatis*.".

Type locality: [Massiliensis] (Marseille/France) (erroneously listed as 'Arabia' by ESCHMEYER 2007).

Genus name: *Cottus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *massiliensis*.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Cottus massiliensis*; the description was accompanied by a diagnosis and description; the name is available as *Cottus massiliensis* Forsskål in Niebuhr, 1775. It was considered by FORSSKÅL to be identical with *Scorpaena scrofa*, and he apparently intended to check the identity of the species before publishing it as a new species. FORSSKÅL differentiated the species from *Cottus cataphractus* (*Agonus*

cataphractus) and *Cottus scorpius* (*Myoxocephalus scorpius*). This species name was clearly not ready for publication, but FABRICIUS in NIEBUHR published it out of FORSSKÅL's manuscript notes. The species was considered as valid by WALBAUM (1792: 393), but is a junior synonym of *Scorpaena porcus* Linnaeus, 1758.

Scorpaena scrofa Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XIV): "10. SCORPÆNA *porcus*. Σκορπήνα. Turc. Scorpis baluk. …".

Localities: "Turc." (probably both İzmir/Turkey, and İstanbul/Turkey).

Turkish name (FORSSKÅL's transcription): Scorpis balük. Actual Turkish name: İskorpit balığı (FRICKE et al. 2007: 77).

Remarks: This species was listed by FORSSKÅL in NIEBUHR as *Scorpaena porcus*, which clearly refers to the Linnaean species *Scorpaena porcus*. However, the species was apparently misidentified, as the Turkish name of *Scorpaena porcus* is 'Lipsoz' (FRICKE et al. 2007: 77). The name 'İskorpit balığı' refers to *Scorpaena scrofa* Linnaeus, 1758, a species which is also common in the Sea of Marmara and Aegean Sea.

Triglidae – Searobins

Chelidonichthys cuculus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[TRIGLA] *cuculus*.".

Locality: "Melita" (La Valletta/Malta).

Chelidonichthys gurnardus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XVI): "32. TRIGLA *gurnardus*. Χελιδωνόψαρο. Turc. *Kirlanidsj-balük*. P. Pect. superne bruneis, fasciis undulatis, obscure cæruleis; margine api, cis dilute cæruleo, subtus virescente.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[TRIGLA] *gurnardus*.".

Localities: "Turc." (?İstanbul/Turkey); "Melita" (La Valletta/Malta).

Actual Turkish name: Benekli kirlangiç (FRICKE et al. 2007: 77).

Remarks: This species is common around both İzmir and İstanbul/Turkey. It was probably collected by FORSSKÅL at İstanbul using the chartered fishing vessel.

Chelidonichthys gurnardus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "TRIGLA *milvus*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "I Taira".

Remarks: *Trigla milvus* Forsskål in Niebuhr, 1775 is a name only (nomen nudum), not accompanied by additional information, and therefore not available. The local name refers to *Chelidonichthys gurnardus* (Linnaeus, 1758).

Chelidonichthys lucernus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[TRIGLA] *lucerna*.".

Locality: "Melita" (La Valletta/Malta). Local name: "I Tigîega".

Trigla lyra Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[TRIGLA] *lyra*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Triglia".

Platycephalidae – Flatheads

Platycephalus indicus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: X): "8. [COTTUS] b) INSIDIATOR. *Rogad*. […, Arabic name]".

FABRICIUS in NIEBUHR (1775a: 25): "8. COTTUS ROGAD; INSIDIATOR.".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.8012 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 13, pl. 2; MØLLER 2006).

Genus name: *Cottus*.

Species name (FORSSKÅL): *insidiator*; (FABRICIUS in NIEBUHR): *rogad*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Rágede, Rogad, Raked.

Remarks: This species was named in two different versions, *Cottus rogad*, *insidiator* in the text on p. 25, and *Cottus insidiator rogad* in the index on p. X, with the name 'Rogad' clearly intended as local Arabic name. Though the name *Cottus rogad*, *insidiator* is not binominal and therefore not available (ICZN, Art. 5), the name is available by indication (ICZN, Art. 12.2.2) as *Cottus insidiator* Forsskål in Niebuhr, 1775 from the index on p. X. A diagnosis and description are found on p. 25, and both versions are linked together by the species code '8'. *Cottus insidiator* was treated as valid since BONNATERRE (1788: 68) and WALBAUM (1792: 392), but is a junior synonym of *Platycephalus indicus* (Linnaeus, 1758).

Perciformes – Perches

Perciformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "CHÆTODON *paru*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: *Chaetodon paru* Forsskål [ex Anonymus] in Niebuhr, 1775 is a name only (nomen nudum), neither accompanied by a diagnosis nor an indication, and therefore not available. The species is unplaceable (PYLE in ESCHMEYER 2007). Under the same name *Chaetodon paru* Bloch, 1787 (BLOCH 1787: 57, pl. 197) was described, which is currently treated as a valid species, with the currently used name *Pomacanthus paru* (Bloch, 1787).

Perciformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[PERCA] *asper*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Perca asper* (non Linnaeus, 1758). The species is unplaceable within the Perciformes.

Perciformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "PERCA *lucioperca*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Perca lucioperca* (non Linnaeus, 1758). The species is unplaceable within the Perciformes.

Perciformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[BLENNIUS] *gunellus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Blennius gunnellus* (non Linnaeus, 1758); the latter has the currently used name *Pholis gunnellus* (Linnaeus, 1758), and is restricted to the north-

eastern Atlantic. FORSSKÅL's Maltese record is unplaceable within the Perciformes.

Perciformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "ANARHICHAS *lupus marinus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a nomen nudum, and a misidentification of *Anarhichas lupus* (non Linnaeus, 1758); the latter species is restricted to the northeastern Atlantic and does not occur south of the North Sea. FORSSKÅL's Maltese record is unplaceable within the Perciformes.

A m b a s s i d a e – Asiatic glassfishes

Ambassis natalensis Gilchrist & Thompson, 1908

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "67. [SCIÆNA] y) SAFGHA; maxilla inferiore longiore.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 53): "67. SCIÆNA SAFGHA; Arab. P. D. duplici $\frac{8}{8}$: immaculata. *Cauda* forsicata. Oblonga, argentea: *Maxillæ* dentatæ; inferior, longior. *Opercula* tenuiter serrata.".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *safgha*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Safgha.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Safgha' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR listed the species *Sciaena safgha* as a new species in the index; he used 'safgha' as the species name in the text, but explicitly mentioned that this is the Arabic name ('Arab.'). The name is accompanied by a diagnosis in the text; as both the index and the text are linked together by the species code '67', the name *Sciaena safgha* Fabricius [ex Forsskål] in Niebuhr, 1775 is therefore not available from the text, but would be available by indication (ICZN, Art. 12.2.2) from the index, with the authorship pending a decision of ICZN. The name was used by subsequent authors as valid, e.g. WALBAUM (1792: 319, *Sciaena safgha*) and BLOCH & SCHNEIDER (1801: 86, *Perca safgha*). This is a rarely used senior synonym of *Ambassis natalensis* Gilchrist & Thompson, 1908 according to ANDERSON & HEEMSTRA (2003: 205). DOR (1984: 94) and GOREN & DOR (1994: 24) used *Sciaena safgha* as a valid name. *Ambassis natalensis* is here retained as the valid name for the species to preserve the name of prevailing usage, but an application to the International Commission on Zoological Nomenclature is needed to reject the senior synonym *Sciaena safgha*.

M o r o n i d a e – Temperate basses

Dicentrarchus sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "GASTEROSTEUS *aculeatus*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[GASTEROSTEUS] *pungitius*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[GASTEROSTEUS] *spinachia*." "L'Ispnotta" (local Maltese name).

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of the three Linnaean species *Gasterosteus aculeatus* (non Linnaeus, 1758), *G. pungitius* (non Linnaeus, 1758) [now named *Pungitius pungitius* (Linnaeus, 1758)], and *G. spinachia* (non Linnaeus, 1758) [now named *Spinachia spinachia* (Linnaeus, 1758)], species restricted to the northeastern Atlantic and northern hemisphere freshwater, not occurring in Malta. According to the vernacular Maltese name (actual name "Spnotta", Anonymus 2007b), the record is based on *Dicentrarchus* spp., probably both *D. labrax* (Linnaeus, 1758) and *D. punctatus* (Bloch, 1792).

Dicentrarchus labrax (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XI): "[42. PERCA h) SUMMANA] γ) *sciaena nilotica* Λάβραξ.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[PERCA] *labrax*.".

FORSSKÅL in NIEBUHR (1775a: 42, part): "... Linn. *Perca nilot.?* Gr. Λάβραξ: quæ certius *Sciæna* est; quia pinna dorsi prima tota in fossa reconditur: & radii Dors. $\frac{7}{7}$? Cauda linearis, ascendens; pinna ani albida, apice fusca.".

Localities: "Nile" (Egypt); "Melita" (La Valletta/Malta).

Remarks: *Sciaena nilotica* (non Linnaeus, 1758) was erroneously diagnosed and described in the synonymy of *Perca summana* (p. XI), or *Perca summana fusco-guttata* (p. 42). This is most probably due to a confusion of FORSSKÅL's species description sheets by FABRICIUS (in NIEBUHR 1775a), as FORSSKÅL apparently decided that this species belonged to the genus *Sciaena* rather than *Perca*. FORSSKÅL's *Sciaena nilotica* (non Linnaeus, 1758) is based on a misidentified *Dicentrarchus labrax* (Linnaeus, 1758). The Linnaean species *Perca nilotica* is a different, valid species of cichlid fishes, with the currently used name *Oreochromis niloticus* (Linnaeus, 1758).

S e r r a n i d a e – Sea basses

Serranidae, indet.

FORSSKÅL in NIEBUHR (1775a: XV): "24. LABRUS a) *striatus*. Πετρόψαρον. Græcorum Literatis: Πέρνυξ.".

Locality: – (Aegean Sea of Turkey or Greece).

Remarks: This is not an independent new name, but a misidentification of *Labrus striatus* (non Linnaeus, 1758); *Centropristis striata* (Linnaeus 1758) is restricted to the West Atlantic. FORSSKÅL's record is based on an unidentified serranid fish, either an *Epinephelus* or a *Mycteroperca*.

"*Aethaloperca rogaa* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "36. PERCA b) ROGAA; subnigra. *Rogáa*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 38–39): "36. [PERCA] ROGAA; *nigro-rufescens; cauda æquali; pinnis nigris: branchiostega & capitis lobis obtectis, obscure-rubris*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Perca*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *rogaa*.

Arabic name (Latinised, FORSSKÅL): Rogáa.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Rogáa' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described *Perca rogaa* as a new species; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and the name would be therefore available as *Perca rogaa* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Aethaloperca rogaa* (Fabricius [ex Forsskål] in Niebuhr,

1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 131) and WALBAUM (1792: 344).

"*Aethaloperca rogaa* (Forsskål in Niebuhr, 1775)"

FORSSKÅL in NIEBUHR (1775a: XI): "37. [PERCA] c) LUNARIA; P. C. macula lunata. *Bint er robbân.*".

FORSSKÅL in NIEBUHR (1775a: 39): "37. PERCA LUNARIA; *ferrugineo-nigra: pinnis pect. nigris, pone flavis: dorsali & caudæ pone hyalino-albis.*".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Perca*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *lunaria*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Bint er robbân.

Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR described this new species using the name *Perca lunaria*; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and the name is therefore available as *Perca lunaria* Forsskål in Niebuhr, 1775. It is a synonym of "*Perca rogaa* Forsskål in Niebuhr, 1775" {would be *Perca rogaa* Fabricius [ex Forsskål] in Niebuhr, 1775}. BONNATERRE (1788: 131), GMELIN (1789: 1315–1316) and WALBAUM (1792: 344) used both names, *Perca rogaa* and *Perca lunaria*, for separate species. GÜNTHER (1859: 97, 116) still treated both names separate, though *Perca lunaria* was considered as doubtful. BLOCH & SCHNEIDER (1801: 334–335) was the first reviewing author giving preference to the name *rogaa*; he treated '*lunaria*' only as a variety of *Bodianus rogaa*. The species is now named "*Aethaloperca rogaa* (Forsskål in Niebuhr, 1775)" (see above). – *Bodianus lunulatus* Shaw [ex Forsskål], 1803 (SHAW 1803: 575) is an unneeded new name for *Perca lunaria* Forsskål in Niebuhr, 1775; it is a junior synonym of "*Perca rogaa* Forsskål".

Cephalopholis argus Bloch & Schneider, 1801

FORSSKÅL in NIEBUHR (1775a: XI): "[41. PERCA g) MINIATA] β) *cæruleo-ocellata*. Bæláb. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 41): "41. [PERCA MINIATA] b) *Varietas*: colore fusco: ocellis cæruleis: P. A. margine postico alba, & P. D. partis inermis margine superiore. Arab. *Baeláh*: vel *Abu beláh* [..., Arabic name]".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.43568 (see KLAUSEWITZ & NIELSEN 1965: 18).

Genus name: *Perca*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *miniata caeruleo-ocellata*.

Arabic names (Latinised, FORSSKÅL): Baeláh, Abu beláh; (FABRICIUS in NIEBUHR): Baeláb.

Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR listed this name as a variety of *Perca miniata* in the index, and gave a brief diagnosis as '*Perca miniata* b) Varietas' in the text on p. 41. As both versions are linked together by the species code '41b', the name is available by indication (ICZN, Art. 12.2.2) as *Perca miniata caeruleoocellata* Forsskål in Niebuhr, 1775, which is a synonym of *Perca miniata* Forsskål in Niebuhr, 1775. Though DOR (1984: 96–97) considered this variety to be a junior synonym of *Cephalopholis minata* (Forsskål in Niebuhr, 1775), FORSSKÅL's description leaves no doubt that it is in fact an unused senior synonym of *Cephalopholis argus* Bloch & Schneider, 1801. An application to the International Commission on Zoological Nomenclature will be needed to retain the currently used latter name. This species was subsequently described as *Perba balah* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 338–339; misspelled *Perca balati* in index on p. 711), which is available and another senior unused synonym of *Cephalopholis argus*; this name needs suppression by the Commission as well.

Cephalopholis miniata (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "41. [PERCA] g) MINIATA; rubra; cæruleo-guttata. Zarbûn. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 41): "41. PERCA MINIATA; *coccineo-rubra, guttis cæruleis undique adspersa: cauda rotundata.*".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Type material: Syntype: ZMUC P.43567 (dry skin) (listed as holotype by MØLLER 2006 and ESCHMEYER 2007) (see KLAUSEWITZ & NIELSEN 1965: 17, pl. 9).

Genus name: *Perca*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *miniata*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Zarbûn, Ataja.

Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR described this species as *Perca miniata*, in the sense of the major variation of the species or *Perca miniata miniata*; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and is therefore available as *Perca miniata* Forsskål in Niebuhr, 1775. The species was treated as valid by BONNATERRE (1788: 131–132) and later authors. KLAUSEWITZ & NIELSEN (1965: 17) discussed the possible mixing of *Perca miniata* and *Perca miniata* var β. For the sake of stability of nomenclature, it is here assumed that FORSSKÅL's syntype ZMUC P.43567 is really meant to be *Perca miniata*, and is herewith designated as the lectotype of the species. This species was subsequently named *Pomacentrus burdi* Lacepède [ex Forsskål, 1775] (LACEPÈDE 1802: 506, 511–512); this name is available, and a junior synonym of *Perca miniata*.

Cephalopholis miniata (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "[41. PERCA g) MINIATA] γ) *cæruleo-guttata, major. Nadjil.*".

FORSSKÅL in NIEBUHR (1775a: 42): "41. [PERCA MINIATA] c) Exstantior est varietas: *rubra, guttis cæruleis*. Arab. *Nadjil* vel *Nâgeu*. ...".

Type locality: "Ad Promont. *Djymûm* ante *Jamboam*" (Ra's Barīdī, NNW Yanbu'/Saudi Arabia, 24°17'N 37°31'E).

Genus name: *Perca*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *miniata caeruleo-guttata*.

Arabic names (Latinised, FORSSKÅL): Nadjil, Nâgeu; (FABRICIUS in NIEBUHR): Nadjil.

Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR listed this name as a variety of *Perca miniata* in the index, and gave a brief diagnosis as '*Perca miniata* c) ... varietas' in the text on p. 42. As both versions are linked together by the species code '41c', the name is available by indication (ICZN, Art. 12.2.2) as *Perca miniata caeruleoguttata* Forsskål in Niebuhr, 1775, which is a synonym of *Perca miniata* Forsskål in Niebuhr, 1775, with the currently used name *Cephalopholis miniatus* (Forsskål in Niebuhr, 1775). The first reviser was GMELIN (1789: 1317), choosing *Perca miniata* as the priority version of the name. This species was subsequently named *Perca nadjil* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 339); this name is available, and a junior synonym of *Perca miniata*.

Epinephelus sp.

FORSSKÅL in NIEBUHR (1775a: XIV): "[110. MUGIL b) CHANOS] β) *magnus. Χάνος*.".

Forsskål in Niebuhr (1775a: 74): "110. [MUGIL chanos] b) Iste, *Anged*, sola magnitudine differt ab alio 3 uln. long. Græc. *Χάνος*. Turc. *Chani*.".
Type locality: – (İstanbul or İzmir, Turkey).
Genus name: *Mugil*.
Species/subspecies name (Forsskål): *chanos magnus*; (Fabricius in Niebuhr): *chanos* (var.).
Greek name: Χάνος; Turkish name: Chani.
Remarks: Forsskål considered this fish first as a variety of his *Mugil chanos*, and named in *Mugil chanos magnus* in the index. Fabricius in Niebuhr also considered it as a variety of *Mugil chanos* in the text, but did not provide a name for the taxon, only calling it variety 'b'. Both versions are linked together by the species code '110b'; but they are neither accompanied by an indication, a diagnosis or a description. The name (which is not included in Eschmeyer 2007) is not available as *Mugil chanos magnus* Forsskål in Niebuhr, 1775; the species cannot be placed within the genus *Epinephelus*. The actual Turkish name 'Hani' refers to *Serranus* or *Epinephelus* sp. (Serranidae) (Fricke et al. 2007); judging from the body size of 3 uln., it must have been based on *Epinephelus* sp.

Epinephelus sp.

Fabricius [ex Forsskål] in Niebuhr (1775a: XV): "26. PERCA? Σελέβαρδο. Arab. *Ugar* vel *Guaza*; aliis *Örsusa*; an idem? P. V. membrana coadunata. Opercula Br. serrata.".
Locality: – (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).
Remarks: Though the name PERCA? Σελέβαρδο is accompanied by a brief diagnosis, it is not available as the species name was not written in Latin letters. The Arabic name 'Guaza' may refer to the species *Perca guaza* (non Linnaeus, 1758). The record is obviously based on an *Epinephelus* sp., probably *Epinephelus marginatus* (Lowe, 1834).

Epinephelus sp.

Fabricius [ex Forsskål] in Niebuhr (1775a: XV): "[26. PERCA? Σελέβαρδο] β) *lilia minor*; forte varietas. Ρεφὸ.".
Locality: – (İstanbul/Turkey, or İzmir/Turkey).
Remarks: This variety name *Perca? Σελέβαρδο lilia minor* Fabricius in Niebuhr, 1775 is not accompanied by a diagnosis, and the species name is not written in Latin characters; therefore, the name is not available. As this was considered as a variety of *Perca? Σελέβαρδο*, the record is probably based on another *Epinephelus* sp. The name was not listed by Eschmeyer (2007).

Epinephelus areolatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "[42. PERCA h) summana] δ) *areolata. Daba.* [..., Arabic name]".
Forsskål in Niebuhr (1775a: 42, part): "42. [PERCA summana] c) Perca areolata; *corpore cinereo, albido; guttis fusco-flavescentibus*.".
Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).
Type material: Holotype: ZMUC P.43570 (dry skin) (see Klausewitz & Nielsen 1965: 18, pl. 10; Møller 2006).
Genus name: *Perca*.
Species/subspecies name (Forsskål, Fabricius in Niebuhr): *summana areolata*.
Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Daba.
Remarks: Forsskål apparently first considered this fish as a variety of *Perca summana*, but later changed the heading to *Perca areolata*. Fabricius in Niebuhr described this name as a variety of *Perca summana* in the index, and as a variety '*Perca areolata*' of the species *Perca summana* in the text; the name is accompanied by a diagnosis and description. The name is available as *Perca summana areolata* Forsskål in Niebuhr, 1775. It was considered as valid since Walbaum (1792: 345–346, *Perca areolata*).

Epinephelus areolatus (Forsskål in Niebuhr, 1775)

Fabricius [ex Forsskål] in Niebuhr (1775a: 44): "*Perca dentibus* Daba. Dentes maxillares laterales, incurvi: superioris maxillæ majores quam palatini, seu interiores: ...".
Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).
Type material: Holotype: ZMUC P.43570 (see Klausewitz & Nielsen 1965: 18, pl. 10).
Genus name: *Perca*.
Species name (Forsskål): –; (Fabricius in Niebuhr): *daba*.
Remarks: In his draft, Forsskål used the Arabic name 'Daba' as a substitute for a Latin name to be selected (which he elsewhere did as '*Perca areolata*'). He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. '*Perca* dentibus *daba*' means 'teeth of *Perca daba*'; this implies that it is a teeth description of the specimen described elsewhere in the paper as *Perca areolata* (see above). Fabricius in Niebuhr thus described the teeth of *Perca daba* as a new species; the name is binominal in both the index and text, it was accompanied by a diagnosis, and would be available as *Perca daba* Fabricius [ex Forsskål] in Niebuhr, 1775, with the authorship pending a decision of ICZN. The name is not mentioned by Eschmeyer (2007). It is an unused synonym of *Epinephelus areolatus* (Forsskål in Niebuhr, 1775), recognisable by the Arabic name 'Daba'. Gmelin (1789: 1317–1318) was the first revising author and chose the name *Perca areolata* as the valid name for the species.

Epinephelus fasciatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "39. [PERCA] e) fasciata. An Perca?".
Forsskål in Niebuhr (1775a: 40): "39. PERCA fasciata; *rubra, fasciis transversis, latis, albidis, sub-quaternis*.".
Type locality: "In *Mari rubro* ad promontorium *Mohammed* hamo capto" (Ras Muhammad, southern Sinai/Egypt, 27°44'N 34°15'E).
Genus name: *Perca*.
Species name (Forsskål, Fabricius in Niebuhr): *fasciata*.
Remarks: Both Forsskål and Fabricius in Niebuhr described this species as *Perca* (?) *fasciata*, indicating in the index and in the remarks that they were not sure if to associate it really with the genus *Perca*. The name is binominal in both the index and text, it was accompanied by a diagnosis and description, and is therefore available as *Perca fasciata* Forsskål in Niebuhr, 1775. This species was treated as valid since Bonnaterre (1788: 131) and Walbaum (1792: 346). *Holocentrus erythraeus* Bloch & Schneider [ex Forsskål], 1801 (Bloch & Schneider 1801: 320) and *Holocentrus forskael* Lacepède [ex Forsskål], 1802 (Lacepède 1802: 337, 376–378) were described as unneeded new names for *Perca fasciata* Forsskål in Niebuhr, 1775; they are junior synonyms.

Epinephelus fuscoguttatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "[42. PERCA h) summana] β) *fusco-guttata. Kassjara*.".
Forsskål in Niebuhr (1775a: 42, part): "42. [PERCA summana] b) Ab hac parum diversa *Varietas*: Fusco-guttata. Corpus cærulescens. ...".
Forrskål localities: "Sues" (As-Suways/Egypt); "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type locality: Sams Pier, Jidda/Jeddah/Juddah, Saudi Arabia (as defined by neotype).
Type material: Neotype: USNM 147594, as selected by RANDALL (1964: 291).
Genus name: *Perca*.
Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *summana fusco-guttata*.
Arabic names (Latinised, FORSSKÅL): Kassjara, Koschar; (FABRICIUS in NIEBUHR): Kassjara.
Remarks: Both FORSSKÅL and FABRICIUS in NIEBUHR listed this name as a variety of *Perca summana* in the index and the text; the name is accompanied by a diagnosis and description. The name is available as *Perca summana fuscoguttata* Forsskål in Niebuhr, 1775, which is a valid species, with the currently used name *Epinephelus fuscoguttatus* (Forsskål in Niebuhr, 1775). This species was subsequently described as *Perca koschar* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 345), which is an available name, and a junior synonym of *Perca summana fuscoguttata*. Parts of FORSSKÅL's remarks ('*Perca nilot.* ...') refer to a different species, the moronid fish *Dicentrarchus labrax* (see above).

Epinephelus marginatus (Lowe, 1834)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[PERCA] *cernua*.".
Locality: "Melita" (La Valletta/Malta). Local Maltese name: "I Cerna".
Remarks: This is a misidentification of *Perca cernua* (non Linnaeus, 1758). According to the Maltese name (actual vernacular Maltese name "Cerna"; Anonymus 2007b), this record has been based on *Epinephelus marginatus* (Lowe, 1834).

"*Epinephelus summana* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "42. [PERCA] h) SUMMANA; albo-guttata; fusca. *Summân*.".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 42): "42. PERCA SUMMANA; *cauda rotundata: corpore cinereo-fusco, guttis albis undique adsperso*.".
Type locality: – (Red Sea).
Type material: Holotype: ZMUC P.43569 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 18, pl. 10; MØLLER 2006).
Genus name: *Perca*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *summana*.
Arabic names (Latinised, FORSSKÅL): Summân, Symman; (FABRICIUS in NIEBUHR): Summân.
Remarks: In his draft, FORSSKÅL used the Arabic name 'Summân' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described *Perca summana* as a new species; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and therefore would be available as *Perca summana* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Epinephelus summana* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid as *Perca summana* since BONNATERRE (1788: 132) and WALBAUM (1792: 345). The name was misspelled *Serranus sumana* by KLUNZINGER (1870: 685).

"*Epinephelus tauvina* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "38. [PERCA] d) TAUVINA; longa, rufo-guttata. *Tauvîna*. [..., Arabic name]".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 39–40): "38. PERCA TAUVINA; *lineari-oblonga, fusca; guttis ferrugineo-nigris in capite, & corpore: cauda rotundata*.".
Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).
Type material: Holotype: ZMUC P.43565 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 17, pl. 8; MØLLER 2006).
Genus name: *Perca*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *tauvina*.
Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Tauvîna.
Remarks: In his draft, FORSSKÅL used the Arabic name 'Tauvîna' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described *Perca tauvina* as a new species; the name is binominal in both the index and text, it was accompanied by a diagnosis and description, and therefore would be available as *Perca tauvina* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Epinephelus tauvina* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 131) and WALBAUM (1792: 340–341).

Serranus cabrilla (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XI): "32. [LABRUS] g) CHANUS; lineatus. Χάνι.".
FORSSKÅL in NIEBUHR (1775a: 36): "32. LABRUS CHANUS; *cauda bifida; capite utrinque rivulis tribus cærulescentibus; quadrato cæruleo sub oculo*.".
Type locality: "CONSTANTINOPOLI" (İstanbul/Turkey).
Genus name: *Labrus*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *lapina*.
Remarks: In his draft, FORSSKÅL used the Greek name Χάνι as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described the new species as *Labrus chanus*; the new name is binominal both in the index and in the text, is accompanied by a diagnosis and description, and would be available as *Labrus chanus* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The species was considered as valid by WALBAUM (1792: 245), but is a junior synonym of *Perca cabrilla* Linnaeus, 1758, with the currently used name *Serranus cabrilla* (Linnaeus, 1758). The Turkish name 'chani' listed by FORSSKÅL corresponds with the modern name 'Hani' (as 'Asil hani', see FRICKE et al. 2007: 80). The species is regularly found in the Bosporus and Marmara Sea near İstanbul; today it is near threatened in Turkey (FRICKE et al. 2007: 80).

Serranus hepatus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[LABRUS] *sachettus*.".
Type locality: "*Melita*" (La Valletta/Malta).
Remarks: The name *Labrus sachettus* Forsskål [ex Anonymus] in Niebuhr, 1775a is a name only (nomen nudum), as it is neither accompanied by a diagnosis nor an indication. Judging from the species name 'sachettus', it is based on *Serranus hepatus* (Linnaeus, 1758), which has the Italian local name 'Sachetto'.

"*Variola louti* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "40. [PERCA] f) LOUTI; cauda bi-falcata. *Louti*. [..., Arabic name]".

Fabricius [ex Forsskål] in Niebuhr (1775a: 40–41): "40. PERCA LOUTI; *oblongo-lanceolata: miniata: guttis pallide-violaceis: cauda bifalcata: pinnarum omnium margine postico flavo.*".
Fabricius [ex Forsskål] in Niebuhr (1775a: 44): "*Perca dentibus* Louti. [..., Arabic name] Dentes incisores nulli. ...".
Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).
Type material: Syntype: ZMUC P.43566 (listed as holotype by Møller 2006 and Eschmeyer 2007) (see Klausewitz & Nielsen 1965: 17, pl. 9).
Genus name: *Perca*.
Species name (Forsskål): –; (Fabricius in Niebuhr): *louti*.
Arabic names (Latinised, Forsskål): Louti; (Fabricius in Niebuhr): Louti, Schân.
Remarks: In his draft, Forsskål used the Arabic name 'Louti' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr described *Perca louti* as a new species; the name is binominal in both the index (p. XI) and the text (pp. 40–41), and the version on p. 44 means 'teeth of *Perca louti*'; the name was accompanied by a diagnosis and description, and therefore would be available as *Perca louti* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Variola louti* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since Bonnaterre (1788: 133) and Walbaum (1792: 338).

Pseudochromidae – Dottybacks

Haliophis guttatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: X): "1. MURÆNA a) GUTTATA. *Sjæeka.*".
Forsskål in Niebuhr (1775a: 22): "1. MURÆNA GUTTATA: *glauca, guttis nigris; macula majori utrinque prope caput.*".
Type locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).
Genus name: *Muraena*.
Species name (Forsskål, Fabricius in Niebuhr): *guttata*.
Arabic name (Latinised, Forsskål): Sjaeka; (Fabricius in Niebuhr): Sjaeaeka (meaning Sjaeka).
Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Muraena guttata*; the name is binominal, and accompanied by a diagnosis and description; the name is available as *Muraena guttata* Forsskål in Niebuhr, 1775, and was treated as valid by Bonnaterre (1788: 35). *Muraena maculata* Lacepède [ex Forsskål], 1800 (Lacepède 1800: 265–266) is an unneeded new name for *Muraena guttata* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Priacanthidae – Bigeyes

"*Priacanthus hamrur* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XI): "44. SCIÆNA a) HAMRUR; squamiceps. *Abu hamrûr.*".
Fabricius [ex Forsskål] in Niebuhr (1775a: 44): "SCIÆNA ... 1) ABU HAMRUR: hujus characterem vide in descriptione".
Fabricius [ex Forsskål] in Niebuhr (1775a: 45): "44. SCIÆNA HAMRUR; cupreo-rubra: pinnis obscurioribus; capite undique squamato: ore subverticali: squamarum margine membranaceo.".
Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).
Type material: Lectotype: ZMUC P.44109 (dry skin, ex ZMUC P.4773), as designated by Klausewitz & Nielsen (1965: 18; see also pl. 11); paralectotype: ZMUC P.44110 (dry skin, ex ZMUC P.4774) (Møller 2006).
Genus name: *Sciaena*.
Species names (Forsskål): –; (Fabricius in Niebuhr): *hamrur*, *abu hamrur*.
Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Abu hamrûr.
Remarks: In his draft, Forsskål used the Arabic name 'hamrur' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) described the new species in two different versions, as *Sciaena hamrur* on pp. 11 and 45, and as *Sciaena abu hamrur* on p. 44. Though the latter version is not binominal and therefore not available (ICZN, Art. 5), the name is accompanied by a diagnosis and description on p. 45, and the version on p. 45 is binominal, thus the name would be available as *Sciaena hamrur* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Priacanthus hamrur* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since Bonnaterre (1788: 122) and Walbaum (1792: 310, *Sciaena abu hamrur*; 313, *Sciaena hamrur*). Bloch & Schneider (1801: 307) erroneously gave the name as *Anthias hamur*.

Apogonidae – Cardinalfishes

Cheilodipterus arabicus (Gmelin [ex Forsskål], 1789)

Forsskål in Niebuhr (1775a: XI): "43. [PERCA] i) LINEATA, lineis nigris. *Djesauvi.*".
Forsskål in Niebuhr (1775a: 42–43): "43. PERCA LINEATA; *pinnis dorsi binis remotis: corpore argenteo, lineis nigris, longitudinalibus; macula caudæ aurea, medio nigra.*".
Locality: "*Djiddæ*" (Jeddah, Juddah/Saudi Arabia).
Remarks: This is not an independent new species description, as proposed by several authors, but an incorrect use of the species *Perca lineata* (non Linnaeus, 1758), based on a misidentification; while the Linnaean *Perca lineata* is based on the haemulid fish *Plectorhinchus lineatus* (Linnaeus, 1758). The first available name for Forsskål's fish is *Perca arabica* Gmelin [ex Forsskål], 1789 (Gmelin 1789: 1312), which is now valid as *Cheilodipterus arabicus* (Gmelin [ex Forsskål], 1789). The name *Cheilodipterus lineatus* does not have the author Forsskål in Niebuhr, 1775, as assumed by several authors. The species was subsequently described as *Perca lineata* by Walbaum (1792: 329–330), and as *Cheilodipterus lineatus* by Lacepède [ex Commerson] (1801: 540, 542, pl. 34, fig. 1), a name considered as a senior synonym of *Centropomus macrodon* which was described by Lacepède [ex Commerson] (1802: 252). *Cheilodipterus lineatus* was believed by several authors to be a secondary homonym of *Perca lineata* Forsskål in Niebuhr, 1775, which is, however, not a species independent from *Perca lineata* Linnaeus, 1758, but a misidentification (see Fricke 1999: 233), as both Forsskål and Niebuhr had the 10th edition of Systema naturae by Linnaeus (1758) readily available (Niebuhr, 1775: 18), but did not give individual credit to the authors of their species names. Both names were frequently used, so the use of *Cheilodipterus lineatus* (Linnaeus, 1758) as the valid name for the species recently named *Cheilodipterus macrodon* by other authors (e. g. Gon & Randall 2003: 32–33), is obligatory.

Sillaginidae – Sillagos

"*Sillago sihama* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "102. [ATHERINA] b) SIHAMA; thoracica. *Sihâmi*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 70): "102. ATHERINA SIHAMA; *pinnis V. subthoracicis; radiis D. pinnæ primæ undecim*.".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen).

Type material: Holotype: ZMUC P.45164 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 27, pl. 38; MØLLER 2006).

Genus name: *Atherina*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *sihama*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Sihâmi, Sjhâmi.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Sihâmi' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. The FORSSKÅL specimen was labelled '*Atherina* sp.' according to KLAUSEWITZ & NIELSEN (1965: 27). FABRICIUS in NIEBUHR described *Atherina sihama* as a new species; the name is binominal in both the index and text; the name was accompanied by a description, and therefore would be available as *Atherina sihama* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Sillago sihama* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 178–179).

Pomatomidae – Bluefishes

Pomatomus saltatrix (Linné, 1766)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "35. PERCA a) LOPHAR, pinnis V. adnatis. Λοφάρι.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 38): "35. PERCA LOPHAR; *argentea; dorso dipterygio; pinnis ventralibus adnatis*.".

Type locality: "CONSTANTINOPOLI" (İstanbul/Turkey).

Genus name: *Perca*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *lophar*.

Turkish name (FORSSKÅL): Lofár balùk.

Actual Turkish name: Lüfer (FRICKE et al. 2007: 83).

Remarks: In his draft, FORSSKÅL used the name 'lofár' or 'lophar' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Perca lophar*. The name is binominal, accompanied by a diagnosis and description, and would be available as *Perca lophar* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The name was considered as valid by WALBAUM (1792: 332), but is a junior synonym of *Pomatomus saltatrix* (Linné, 1766).

Coryphaenidae – Dolphinfishes

Coryphaena hippurus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "CORYPHÆNA *hippurus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "I Lampuca".

Remarks: The actual vernacular Maltese name of this species is "Lampuka" (Anonymus 2007b).

Echeneidae – Remoras

Echeneis naucrates Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XIV): "7. ECHENEIS *neucrates*. Djiddæ *Keide* [..., Arabic name] vel *Kaml el Kersch*; [..., Arabic name] id est: *pediculus Squali Carebar*, quia sæpe adhæret tenaciter huic pisci, Lohajæ *Keda*.".

Localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Remarks: This is clearly the Linnaean name *Echeneis neucrates* or *E. naucrates* Linnaeus, 1758. In the area, species attached to sharks are either *Echeneis naucrates* Linnaeus, 1758 or *Remora remora* (Linnaeus, 1758), both of which were known to LINNAEUS (1758) and should have been identifiable for FORSSKÅL, so it is assumed that the identification was correct.

Remora remora (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "ECHENEIS *remora*.".

Locality: "Melita" (La Valletta/Malta).

Carangidae – Jacks

Carangidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[ZEUS] *gallus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "I Serduk".

Remarks: This is a misidentification of *Zeus gallus* (non Linnaeus, 1758); *Selene gallus* (Linnaeus, 1758) is a West Atlantic species and does not occur in the Mediterranean Sea. As the name is listed without diagnosis or indication, the record cannot be assigned to genus or species level.

"*Alepes djedaba* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "75. [SCOMBER] g) DJEDABA; cauda sine carinis. *Djedaba*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 56–57): "75. SCOMBER DJEDABA; *albus, lateribus & caudæ pinna flavis*.".

Type localities: "LOHAJÆ." (Al-Luhayya/Yemen); "DJIDDÆ." (Jeddah, Juddah/Saudi Arabia); "SUES" (As-Suways/Egypt).

Type material: Syntype: ZMUC P.46441 (dry skin) (erroneously listed as holotype by KLAUSEWITZ & NIELSEN 1965: 22, pl. 26; MØLLER 2006; ESCHMEYER 2007).

Genus name: *Scomber*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *djedaba*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Susnok, Djedaba, Bajad.

Remarks: In his draft, FORSSKÅL used the Arabic name 'djedaba' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described it as *Scomber djedaba* in both the index and text; the name is accompanied by a diagnosis and description, and would be available as *Scomber djedaba* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Alepes djedaba* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since

Bonnaterre (1788: 142) and Walbaum (1792: 219). This species was subsequently described as *Scomber albus* Gmelin [ex Forsskål], 1789 (Gmelin 1789: 1334), which is a junior synonym of "*Scomber djedaba* Forsskål in Niebuhr, 1775". The name was misspelled as *Caranx djeddaba* by Rüppell (1830: 97, pl. 25, fig. 3) and Klunzinger (1871: 458).

Carangoides armatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XII): "68. [SCIÆNA] z) armata; nucha spinifera. *Galemfish.*".

Fabricius [ex Forsskål] in Niebuhr (1775a: 53): "68. SCIÆNA? armata, galemfish. Facies Scombri. …".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species names (Forsskål): *armata*; (Fabricius in Niebuhr): *armata*, *galemfish*.

Arabic name (Latinised, Forsskål): Galemfish.

Remarks: Forsskål intended to describe this species as *Sciaena armata*, and this is how it was named in the index on p. XII, but he was uncertain about the generic affiliation, and only doubtfully included it in *Sciaena*. Fabricius in Niebuhr described the species on p. 53 as *Sciaena armata*, *galemfish*. As Fabricius in Niebuhr (1775a) described two alternative names for the species, *armata* or *galemfish*, he did not clearly decide how to name the species, so the version on p. 53 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '68'; the name on p. XII is thus accompanied by a brief description, and is available by indication (ICZN, Art. 12.2.2) as *Sciaena armata* Forsskål in Niebuhr, 1775. *Sciaena armata* was treated as valid since Bonnaterre (1788: 125) and Walbaum (1792: 319).

"*Carangoides bajad* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XII): "[71. SCOMBER c) ferdau] β) linea laterali elata, carinata. *Bajad.*".

Fabricius [ex Forsskål] in Niebuhr (1775a: 55): "71. [SCOMBER ferdau] b) bajad; *Varietas. Opercula* anteriora obesa. …".

Type locality: – (Red Sea).

Type material: Syntypes: ZMUC P.46437–46438 (2 dry skins, head of smaller specimen missing) (see Klausewitz & Nielsen 1965: 22, pl. 25; Møller 2006).

Genus name: *Scomber*.

Species/subspecies name (Forsskål): –; (Fabricius in Niebuhr): *ferdau bajad*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Bajad; (Fabricius in Niebuhr): Abu sænsun, Hælj.

Remarks: In his draft, Forsskål used the Arabic name 'bajad' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) described it as a new variety in two versions, as *Scomber ferdau* var. β in the index on p. XII, and as *Scomber ferdau bajad* on p. 55 The name is accompanied by a short description, and would be available as *Scomber bajad* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Carangoides bajad* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. This species was treated as valid since Walbaum (1792: 220).

"*Carangoides ferdau* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XII): "71. [SCOMBER] c) ferdau; quinque-fasciatus. *Ferdau.*".

Fabricius [ex Forsskål] in Niebuhr (1775a: 55): "71. SCOMBER ferdau; *ovali-oblongus, argenteus, guttis aureis lateralibus; fasciis transversis fuscis quinque, obsoletis.*".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: No types known. A specimen with the label saying holotype (ZMUC P.46442, as figured in Klausewitz & Nielsen 1965: 22, pl. 27; Møller 2006) is not this species.

Genus name: *Scomber*.

Species name (Forsskål): –; (Fabricius in Niebuhr): *ferdau*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Ferdau.

Remarks: In his draft, Forsskål used the Arabic name 'ferdau' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) described it as a new species as *Scomber ferdau*. The name is binominal in both the index and text, is accompanied by a diagnosis and description, and would be available as *Scomber ferdau* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Carangoides ferdau* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since Bonnaterre (1788: 141) and Walbaum (1792: 219–220).

Carangoides fulvoguttatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XII): "73. [SCOMBER] e) fulvoguttatus. *Gæzz.* […, Arabic name]".

Forsskål in Niebuhr (1775a: 56): "73. SCOMBER fulvo-guttatus; simillimus (S. 71) [*Scomber ferdau*] *guttis* aureis per latera frequentibus, orbiculatis, inordinatis; …".

Type locality: – (Red Sea).

Genus name: *Scomber*.

Species name (Forsskål, Fabricius in Niebuhr): *fulvo-guttatus*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Gæzz.

Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Scomber fulvo-guttatus*; the name is binominal, and accompanied by a diagnosis and description; it is available as *Scomber fulvoguttatus* Forsskål in Niebuhr, 1775. The species has been treated as valid since Walbaum (1792: 220). *Caranx gaess* Lacepède [ex Forsskål], 1801 (Lacepède 1801: 59, 75–76, misspelled *Caranx gaezz* on p. 59) is an unneeded new name for *Scomber fulvoguttatus* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Caranx ignobilis (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XII): "72. [SCOMBER] d) ignobilis; argenteo-cærulescens. *Kirb.* […, Arabic name]".

Fabricius [ex Forsskål] in Niebuhr (1775a: 55–56): "72. SCOMBER ignobilis, kirm; *argenteus; dorso cærulescente: pinnis pectoralibus & ventralibus rufescentibus.*".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Type material: Syntypes: ZMUC P.46439–46440 (2 dry skins, extremely poor condition) (see Klausewitz & Nielsen 1965: 22, pl. 26; Møller 2006).

Genus name: *Scomber*.

Species names (Forsskål): *ignobilis*; (Fabricius in Niebuhr): *ignobilis*, *kirm*.

Arabic names (Latinised, Forsskål): Kirm, Djarm, Girb, Kórab (smaller), Djim (larger); (Fabricius in Niebuhr): Kirb.

Remarks: Forsskål intended to describe this species as *Scomber ignobilis*, and this is how it was named in the index on p. XII. Fabricius in Niebuhr described the species on pp. 54–55 as *Scomber ignobilis*, *kirm*. As Fabricius in Niebuhr (1775a) described two alternative names for the species, *ignobilis* or

kirm, he did not clearly decide how to name the species, so the version on pp. 55–56 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '72'; the name on p. XII is thus accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Scomber ignobilis* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 142) and WALBAUM (1792: 218).

Caranx ignobilis (Forsskål in Niebuhr, 1775)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "74. [SCOMBER] f) SANSUN; immaculatus. *Abu sansun*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 56): "74. SCOMBER SANSUN; *argenteo-nitens, immaculatus; caudæ carina elata, æquali*.".

Type locality: "LOHAJÆ." (Al-Luhayya/Yemen).

Genus name: *Scomber*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *sansun*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu sansun, Abu læjla, Baghe, Dheirak, Bockas.

Remarks: In his draft, FORSSKÅL used the Arabic name 'sansun' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described it as *Scomber sansun* in both the index and text; the name is binominal, accompanied by a diagnosis and description, and would be available as *Scomber sansun* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. It was treated as valid by BONNATERRE (1788: 142) and WALBAUM (1792: 217). According to C. B. KLUNZINGER (unpublished manuscript, SMNS, ca. 1883), *Scomber sansun* is a junior synonym of *Caranx ignobilis* (Forsskål in Niebuhr, 1775).

Gnathanodon speciosus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "70. [SCOMBER] b) SPECIOSUS; aureus, fasciis nigris alternis. *Rîm*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 54–55): "70. SCOMBER RIM, SPECIOSUS; *pallide aureus; fasciis verticis obliquis; corporis septem nigris, alternis*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Scomber*.

Species names (FORSSKÅL): *speciosus*; (FABRICIUS in NIEBUHR): *rim*, *speciosus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Rîm.

Remarks: FORSSKÅL intended to describe this species as *Scomber speciosus*, and this is how it was named in the index on p. XII. FABRICIUS in NIEBUHR described the species on pp. 54–55 as *Scomber rim*, *speciosus*. As FABRICIUS in NIEBUHR (1775a) described two alternative names for the species, *rim* or *speciosus*, he did not clearly decide how to name the species, so the version on pp. 54–55 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '70'; the name on p. XII is thus accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Scomber speciosus* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 143) and WALBAUM (1792: 217–218).

Lichia amia (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SCOMBER] *amia*.".

Locality: "Melita" (La Valletta/Malta).

"*Scomberoides lysan* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "69. SCOMBER a) LYSAN; spinis d. 7, distinctis. *Lysan*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 54): "69. SCOMBER LYSAN; *albido-maculatus; spinis dorsalibus septem primis separatis*.".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Type material: Lectotype: ZMUC P.46435 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 22; see also pl. 25); paralectotype: ZMUC P.46436 (dry skin) (MØLLER 2006).

Genus name: *Scomber*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *lysan*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Myssiæf, Lysan, Öbri.

Remarks: In his draft, FORSSKÅL used the Arabic name 'lysan' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described it as a new species as *Scomber lysan*. The name is binominal in both the index and text, is accompanied by a diagnosis and description, and would be available as *Scomber lysan* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Scomberoides lysan* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid by BONNATERRE (1788: 140), GMELIN (1789: 1325, *Gasterosteus lysan*), and WALBAUM (1792: 216–217). *Centronotus lyzan* is not an independent species description, but an incorrect subsequent spelling by LACEPÈDE (1801: 309, 316–317).

Trachinotus blochii (Lacepède [ex Commerson], 1801)

FORSSKÅL in NIEBUHR (1775a: XII): "76. [SCOMBER] h) FALCATUS; pinna dorsi & ani falcata. *Hogel*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 57): "76. SCOMBER FALCATUS; *rhomboidalis; pinna secunda dorsi & ani falcata*.".

Localities: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); "LOHAJÆ" (Al-Luhayya/Yemen).

FORSSKÅL material (no types as no new species description): NRM 16675 (1 dry), ZMUC P.46444 and 46445 (2 dry skins) (see KLAUSEWITZ & NIELSEN 1965: 22; MØLLER 2006).

Remarks: This is not an independent species description, but a misidentification of *Labrus falcatus* (non Linnaeus, 1758), which was here placed in the genus *Scomber* [currently used name *Trachinotus falcatus* (Linnaeus, 1758)]. The subsequent usage as *Scomber falcatus* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 142–143) and other authors is neither available. The first available name of the species is *Caesiomorus blochii* Lacepède [ex Commerson], 1801, with the currently used name *Trachinotus blochii* (Lacepède [ex Commerson], 1801).

Trachinotus ovatus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SCOMBER] *glaucus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This record is based on *Scomber glaucus* Linnaeus, 1758, which is a synonym of *Gasterosteus ovatus* Linnaeus, 1758.

Trachurus mediterraneus (Steindachner, 1868)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SCOMBER] *trachurus*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Savrella".

Remarks: The actual vernacular Maltese name is "Sawrella ghajnejh kbar" (Anonymus 2007b).

Trachurus ponticus Aleev, 1956

FORSSKÅL in NIEBUHR (1775a: XVI): "29. [SCOMBER] c) *trachurus*. Σταυρίδια. Turc. *Staurit-balük*. Spina ante pinnam D. primam, tecta cute tam tenera, ut sæpe prorumpat & videatur nuda.".

Locality: – (İstanbul/Turkey).

Actual Turkish name: İstavrit (FRICKE et al. 2007: 85).

Remarks: This is a misidentification of the species *Scomber trachurus* (non Linnaeus, 1758); according to the Turkish name, the record is based on *Trachurus ponticus* (Aleev, 1956), a species which is a migrant regularly found in shallow water around İstanbul. The specimen recorded by FORSSKÅL was probably collected by the fishing vessel which he chartered in Constantinople/İstanbul.

L e i o g n a t h i d a e – Ponyfishes

Leiognathus berbis (Valenciennes [ex Forsskål] in Cuvier & Valenciennes, 1835)

FORSSKÅL in NIEBUHR (1775a: XII): "[77. SCOMBER e) EQUULA] β) minimus. *Melliet*.".

FORSSKÅL in NIEBUHR (1775a: 58): "77. [SCOMBER EQUULA] b); DJIDDÆ *Melliet*; LOHAJÆ *Berbîs*; [..., Arabic name] A priore differt: *Magnitudine*; ...".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Genus name: *Scomber*.

Species/subspecies name (FORSSKÅL): *equula minimus*; (FABRICIUS in NIEBUHR): –.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Melliet, Berbîs.

Remarks: This species was described by FORSSKÅL and FABRICIUS in NIEBUHR in two versions, as *Scomber equula minimus* in the index on p. XII, and as *Scomber equula* var. 'b' in the text on p. 58. Both versions are linked together by the species code '77b'; the name is therefore accompanied by a diagnosis/description, and is available by indication (ICZN, Art. 12.2.2) as *Scomber equula minimus* Forsskål in Niebuhr, 1775. Unfortunately, this is an unused senior synonym of the species described as *Equula berbîs* by VALENCIENNES [ex FORSSKÅL] in CUVIER & VALENCIENNES (1835: 85), with the latter name being an unnecessary new name for *Scomber equula minimus* of FORSSKÅL in NIEBUHR (1775a). The unused name *Scomber equula minimus* is here rejected according to the preamble and Art. 23.2 of ICZN; however, a petition to the International Commission on Zoological Nomenclature will be needed to suppress the name *Scomber equula minimus* Forsskål in Niebuhr, 1775 and retain the name *Equula berbis* Valenciennes [ex Forsskål] in Cuvier & Valenciennes, 1835 for this species, which is currently considered as valid, with the currently used name *Leiognathus berbis* (Valenciennes [ex Forsskål] in Cuvier & Valenciennes, 1835). The species was subsequently named *Scomber melliet* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 220–221); this is another senior synonym of *Equula berbis*, and needs suppression by the Commission as well.

Leiognathus equulus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "77. [SCOMBER] e) EQUULA; gibbo duplici. *Abu kurse*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 58): "77. SCOMBER EQUULA; *pinnulis pinnaque dorsi connatis*.".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.48219 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 23); paralectotype: ZMUC P.48220 (dry skin) (MØLLER 2006).

Genus name: *Scomber*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *equula*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu kurse.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scomber equula*; the name is binominal in both the index and text, is accompanied by a diagnosis, and is therefore available as *Scomber equula* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 141) and WALBAUM (1792: 220).

L u t j a n i d a e – Snappers

Lutjanus argentimaculatus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "50. [SCIÆNA] g) ARGENTIMACULATA; dentibus fastigiatis. *Scháafen*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 47–48): "50. SCIÆNA ARGENTIMACULATA; Arab. Scháafen. [..., Arabic name].".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species name (FORSSKÅL): *argentimaculata*; (FABRICIUS in NIEBUHR): *argenti-maculata*, *argentimaculata*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Scháafen.

Remarks: This new species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Sciaena argentimaculata*. The name is binominal in both the index and text, accompanied by a diagnosis and description, and available as *Sciaena argentimaculata* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 123) and WALBAUM (1792: 313). *Sciaena argentata* Gmelin [ex Forsskål], 1789 (GMELIN 1789: 1300–1301) is an unneeded new name for *Sciaena argentimaculata* Forsskål in Niebuhr, 1775, and a junior synonym. *Perca argentata* of BLOCH & SCHNEIDER (1801: 86) is not an independent new species description, but a change of the generic assignment of *Sciaena argentata* Gmelin; it cannot be treated as a primary homonym of *Perca argentata* Bloch, 1792 (BLOCH 1792: 86, pl. 311, fig. 1) from Japan.

"*Lutjanus bohar* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "47. [SCIÆNA] d) BOHAR; dorso recto. *Bohar*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44): "SCIÆNA ... 2) HOBAR. a) OMNES HÆ SCIÆNÆ MACULA GAUDENT NIGRA SUB JUNCTURA PINNARUM DORS. b) IMMACULATÆ. ...".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 46): "47. SCIÆNA BOHAR; *rubens, lineis nebulisve albidis*.".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.4779 (see KLAUSEWITZ & NIELSEN 1965: 19, pl. 14; MØLLER 2006).

Genus name: *Sciaena*.

Species names (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *bohar*, *hobar*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Bohár, Bhâr.

Remarks: In his draft, FORSSKÅL used the Arabic name 'bohár' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described it as a new species in two different versions, as *Sciaena bohar* on

pp. XI and 46, and as *Sciaena hobar* on p. 44. Most probably *Sciaena hobar* is a spelling error. The name *Sciaena bohar* is binominal in both the index and text, accompanied by a diagnosis and description, and would be available as *Sciaena bohar* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Lutjanus bohar* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. This species was treated as valid since Bonnaterre (1788: 122–123) and Walbaum (1792: 314).

Lutjanus fulviflamma (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "45. SCIÆNA b) fulviflamma. *Abu noqta*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 45–46): "45. SCIÆNA fulviflamma; *pinnis dorsalibus connexis; flavicans, macula laterali nigra: vittis longitudinalibus aureis*.".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.4775 (dry skin), as designated by Klausewitz & Nielsen (1965: 18; see also pl. 12); paralectotype: ZMUC P.4776 (dry skin) (Møller 2006).

Genus name: *Sciaena*.

Species name (Forsskål, Fabricius in Niebuhr): *fulviflamma*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Abu noqta, Håbar, Hober.

Remarks: This new species was described by both Forsskål and Fabricius in Niebuhr as *Sciaena fulviflamma*. The name is binominal in both the index and text, accompanied by a diagnosis and description, and available as *Sciaena fulviflamma* Forsskål in Niebuhr, 1775; it was treated as valid since Bonnaterre (1788: 120) and Walbaum (1792: 316). *Centropomus hober* Lacepède [ex Forsskål], 1802 (Lacepède 1802: 248, 255–256, 263–264) is an unneeded new name for *Sciaena fulviflamma* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Lutjanus gibbus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "48. [SCIÆNA] e) gibba; dorso gibbo. *Nagil*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 46–47): "48. SCIÆNA gibba; *rubens, albo-guttata, dorso gibbo*.".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species name (Forsskål, Fabricius in Niebuhr): *gibba*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Nagil, Naqil, Asmûdi.

Remarks: This new species was described by both Forsskål and Fabricius in Niebuhr as *Sciaena gibba*. The name is binominal in both the index and text, accompanied by a diagnosis and description, and available as *Sciaena gibba* Forsskål in Niebuhr, 1775; the species was treated as valid since Bonnaterre (1788: 123) and Walbaum (1792: 314). – *Sciaena gibbosa* of Shaw (1803: 539) is not an independent species description, but a spelling error for *Sciaena gibba*.

"*Lutjanus kasmira* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XI): "46. [SCIÆNA] c) kasmira; quadrivittata. *Kasjmiri*.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 46): "46. SCIÆNA kasmira; *flavescens, vittis utrinque cœruleis quatuor majoribus*.".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.4777 (dry skin), as designated by Klausewitz & Nielsen (1965: 18; see also 11–19, pl. 13); paralectotype: ZMUC P.4778 (dry skin) (Møller 2006).

Genus name: *Sciaena*.

Species name (Forsskål): –; (Fabricius in Niebuhr): *kasmira*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Kasjmiri, Tyrki.

Remarks: In his draft, Forsskål used the Arabic name 'Kasjmiri' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) described *Sciaena kasmira* as a new species; it is binominal in both the index and text, accompanied by a diagnosis and description, and would be available as *Sciaena kasmira* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Lutjanus kasmira* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. This species was treated as valid since Bonnaterre (1788: 122) and Walbaum (1792: 314–315).

Macolor niger (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI): "49. [SCIÆNA] f) nigra. *Gatîe*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 47): "49. SCIÆNA nigra; *tota nigra, ventre fusco-albescente*.".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype (or syntype): ZMUC P.4780 (see Klausewitz & Nielsen 1965: 19, pls. 14–15; Møller 2006). Another Forsskål specimen attributed to *Sciaena nigra* (ZMUC P.4781), which may be another syntype, is based on *Lutjanus* sp.

Genus name: *Sciaena*.

Species name (Forsskål, Fabricius in Niebuhr): *nigra*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Gatîe.

Remarks: This new species was described by both Forsskål and Fabricius in Niebuhr as *Sciaena nigra*. The name is binominal in both the index and text, accompanied by a diagnosis and description, and available as *Sciaena nigra* Forsskål in Niebuhr, 1775; the species was treated as valid by Bonnaterre (1788: 123) and later authors.

Gerreidae – Mojarras

"*Gerres oeyena* (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XI): "29. [LABRUS] d) öyena; labio prolabente. *Abu öyena* vel *Kuvêr*. [..., Arabic name] Lohajæ.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 35): "29. LABRUS öyena; *corpore argenteo; radiis dorsalibus 2–5 subinermibus*.".

Type localities: "Lohajæ" (Al-Luhayya/Yemen); "Sues" (As-Suways/Egypt); "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: Lectotype: ZMUC P.48209 (listed as holotype by Eschmeyer 2007), selected by Klausewitz & Nielsen 1965: 16; see also 16–17, pl. 7; Møller 2006).

Genus name: *Labrus*.

Species name (Forsskål, Fabricius in Niebuhr): *öyena*.

Arabic names (Latinised, Forsskål): Abu öyena, Kuvêr.

Remarks: In his draft, Forsskål used the Arabic name 'öyena' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr described the new species as *Labrus öyena*; as the 'ö' is the Latin equivalent of 'oe', the species name must be spelled '*oeyena*'. The name is binominal both in index and text, is accompanied by a diagnosis and description, and therefore would be available as *Labrus*

oeyena Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Gerres oeyena* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 241, *Labrus Oeyena*; 291, *Labrus Oyena*, misspelling in index). Two additional paralectotypes (ZMUC P.48210–48211) were identified as *Gerres argyreus* (Bloch & Schneider, 1801) by KLAUSEWITZ & NIELSEN (1965: 16–17), which is also a junior synonym of *Gerres oeyena*. BLOCH & SCHNEIDER (1801: 245) erroneously spelled the name *Labrus oeyna*.

Gerres longirostris (Lacepède [ex Commerson], 1801)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "29. [LABRUS d) ÖYENA] β) *Gasa*; [..., Arabic name] vittis rubris.".

FORSSKÅL in NIEBUHR (1775a: 35): "29b. [LABRUS ÖYENA] b) Huic maxime affinis *alius Vittis rubris, interruptis*. Hic Ar. *Gasa:* [..., Arabic name] prior *Abu Öyena*. ...".

Type locality: – (Red Sea, Al Luhayya/Yemen?).

Genus name: *Labrus*.

Species/subspecies name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *öyena gasa*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Gasa.

Remarks: In his draft, FORSSKÅL used the Arabic name 'gasa' as a substitute for a Latin name to be selected for a subspecies of *Labrus* (*öyena*). He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the new taxon as *Labrus öyena gasa* in the index on p. XI, but omitted the subspecies name on p. 35 and only cited it as the Arabic name. ESCHMEYER (2007) believes the name is not available as it was listed without a scientific name. However, the name is described as a subspecies name in the index, and accompanied by a diagnosis there; the species was not collected at Gasa, as ESCHMEYER stated, but 'Gasa' was the Arabic name. Despite the fact that it is not mentioned explicitly in the text on p. 35, a little more detail is given there, and both index and text are linked together; the name would be available by indication (ICZN, Art. 12.2.2) from the subspecies description in the index as *Labrus oeyena gasa* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN (considered as valid as *Labrus gasa* by WALBAUM 1792: 241). According to the diagnosis, this is an unused senior synonym of *Labrus longirostris* Lacepède [ex Commerson], 1801, which has the currently used name *Gerres longirostris* (Lacepède [ex Commerson], 1801). In order to preserve the latter name, a petition to the International Commission on Zoological Nomenclature will be needed.

Haemulidae – Grunts

"*Plectorhinchus gaterinus* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "[59. SCIÆNA] q) GATERINA; fusco-guttata *Gaterîn*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 45): "SCIÆNA ... 6) GATERIN, operculis posterioribus inermibus.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 50): "59. SCIÆNA GATERINA; *flavido-cærulescens, nigro-guttata, maculis sparsis*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Lectotype: ZMUC P.48212 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 20; see also pl. 18); paralectotype: ZMUC P.48213 (dry skin) (MØLLER 2006).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *gaterina*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Gaterîn.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Gaterîn' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Sciaena gaterina*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and would be available as *Sciaena gaterina* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Plectorhinchus gaterinus* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 124) and WALBAUM (1792: 315). *Sciaena gaterin* of Fabricius [ex Forsskål] in Niebuhr (1775a: 45) is a misspelling of *Sciaena gaterina*.

"*Plectorhinchus gaterinus* (Forsskål in Niebuhr, 1775)"

FORSSKÅL in NIEBUHR (1775a: XII): "[59. SCIÆNA GATERINA] β) *gaterina minor*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 51): "59. [SCIÆNA GATERINA] b) SCIÆNA ABU-MGATERIN; [..., Arabic name] *vittis fuscis, utrinque quatuor, nigro guttatis, pinnis flavis*.".

Type locality: – (Red Sea).

Type material: Syntypes: ZMUC P.48216 (1 dry skin); ZMUC P.48217 (1 dry skin) (see KLAUSEWITZ & NIELSEN 1965: 20; MØLLER 2006).

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): *gaterina minor*; (FABRICIUS in NIEBUHR): *abu-mgaterin*.

Arabic name (Latinised, FORSSKÅL): Abu Mgaterin.

Remarks: In his draft, FORSSKÅL apparently used the subspecies *Sciaena gaterina minor* for this taxon, as listed in the index on p. XII. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Sciaena abu-mgaterin*, obviously confusing the Arabic name with the species name. *Sciaena gaterina minor* is linked to *Sciaena abu-mgaterin* on p. 51 by the species code '51b'; it is therefore accompanied by a diagnosis and description, and would be available by indication (ICZN, Art. 12.2.2) as *Sciaena gaterina minor* Forsskål in Niebuhr, 1775 (which is not included in ESCHMEYER 2007), the authorship pending a decision of ICZN. This species was considered to be valid by WALBAUM (1792: 315, *Sciaena abu-mgaterin*), but is a synonym (the juvenile form) of "*Plectorhinchus gaterinus* (Forsskål in Niebuhr, 1775)". GMELIN (1789: 1303) was the first reviser, choosing *Sciaena gaterina* as the senior synonym.

Plectorhinchus schotaf (Walbaum [ex Forsskål], 1792)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "[59. SCIÆNA GATERINA] γ) media maxilla edentula. *Schotaf*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 51): "59. [SCIÆNA GATERINA] c) SCHOTAF [..., Arabic name] vel SOFAT Arab.".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.48214 (dry skin, listed as holotype by MØLLER 2006), as designated by KLAUSEWITZ & NIELSEN (1965: 20; see also pl. 19); paralectotype: ZMUC P.48215 (dry skin).

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): – (*schotaf* or *sofat* as Arabic names).

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Schotaf, Sofat.

Remarks: Neither FORSSKÅL nor FABRICIUS in NIEBUHR provided a name for this form; they described it as *Sciaena gaterina* γ in the index on p. XII, and *Sciaena gaterina* c) on p. 51. The name 'Schotaf' is clearly marked as Arabic name in the index, separated from the species name by a diagnosis; 'Schotaf' or 'Sofat' are clearly marked as Arabic names, and not scientific species/subspecies names, in the text on p. 51, and even if 'schotaf' would be interpreted as a species/subspecies name, it would not be available because FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a) would then have described it as either *Sciaena gaterina schotaf* **or** *Sciaena gaterina sofat*, and therefore did not clearly decide which name they intended to use. GMELIN (1789: 1303) listed *Sciaena Sofat* as a junior synonym of *Sciaena Gaterina*, which makes his *Sciaena sofat* not available as mentioned in synonymy, and not considered as valid by subsequent authors (ICZN, Art. 11.5, 11.6.2). The first available version of the name is as *Sciaena schotaf* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 315). It is a valid species with the currently used name *Plectorhinchus schotaf* (Walbaum [ex Forsskål], 1792). The name was misspelled as *Diagramma shotaf* by RÜPPELL (1830: 126).

Plectorhinchus schotaf (Walbaum [ex Forsskål], 1792)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "[59. SCIÆNA q) GATERINA] δ) FÆTELA: [..., Arabic name] maxima.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 50–51): "59. [SCIÆNA GATERINA] ... d) FÆTELA; [..., Arabic name] Dentes, Labia, Nares, Oculi, Vertex, Cauda, Squamæ priorum [*Sciæna schotaf*]. Opercula anteriora non sinuata, subtus integra. *Spina* A. secunda longior & crassior tertia. *Color* fuscus, venter albidus, immaculatus. ...".

Type locality: – (Red Sea, probably Jeddah).

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *gaterina faetela*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Faetela.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Faetela' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the subspecies as *Sciaena gaterina faetela*; the name is accompanied by a diagnosis and description, and would be available as *Sciaena faetela* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN; judging on the description, it is conspecific with *Plectorhinchus schotaf* (Walbaum [ex Forsskål], 1792), which is a major problem as it would be a senior synonym of that species. In order to preserve stability of nomenclature, a petition to the International Commission on Zoological Nomenclature will be necessary to suppress the name *Sciaena faetela* Fabricius [ex Forsskål] in Niebuhr, 1775. This species was subsequently misspelled *Diagramma fatela* by RÜPPELL (1830: 126), and *Diagramma foetela* by KLUNZINGER (1870: 737–738). This species was subsequently named *Sciaena maxima* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 318–319); this is another synonym of *Plectorhynchus schotaf* and needs suppression by the Commission as well.

Pomadasys argenteus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "60. [SCIÆNA] r) ARGENTEA; nigro-guttata. *Nagem*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 51): "60. SCIÆNA ARGENTEA, NAGEB; *guttis nigris in corporis dimidio superiori*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); – "Alis" (Red Sea).

Type material: Syntype: ZMUC P.48218 (dry skin) (listed as holotype by ESCHMEYER 2007) (see KLAUSEWITZ & NIELSEN 1965: 20–21, pls. 19–20; MØLLER 2006).

Genus name: *Sciaena*.

Species names (FORSSKÅL): *argentea*; (FABRICIUS in NIEBUHR): *argentea*, *nageb*.

Arabic name (Latinised, FORSSKÅL): Nagem; (FABRICIUS in NIEBUHR): Nageb.

Remarks: FORSSKÅL planned to name this species *Sciaena argentea*, and this is how the species is listed in the index on p. XII. FABRICIUS in NIEBUHR described it in the text on p. 51 as *Sciaena argentea*, *nageb*. The name is binominal in the index, but in the text, two alternative names are proposed, *argentea* or *nageb*. Both index and text are linked together by the species code '60'; the name is accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Sciaena argentea* Forsskål in Niebuhr, 1775 (*Sciaena nageb*, however, is not available). This species was considered as valid since WALBAUM (1792: 317–318). The species was subsequently named *Sciaena nageb* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 121), which is a junior synonym. The *Pristipoma nageb* of RÜPPELL (1838: 124, pl. 30, fig. 2) is not an independent new species description (as erroneously assumed by ESCHMEYER 2007), but based in part on FORSSKÅL in NIEBUHR's description, and on BONNATERRE's *Sciaena nageb*. – *Perca argentata* Bloch & Schneider [part: ex Gmelin, Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 86) was subsequently based on this species and on *Sciaena argentimaculata* (see above, *Lutjanus argentimaculatus*), and is an unneeded junior synonym of the latter species; it is also a primary homonym of *Perca argentata* Bloch, 1792 (BLOCH 1792: 86, pl. 311, fig. 1) from Japan.

Pomadasys stridens (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "58. [SCIÆNA] p) STRIDENS. *Korkor*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 50): "58. SCIÆNA STRIDENS; Arab. *Korkor* vel *Gorgor* [..., Arabic name]".

FORSSKÅL locality: – (Red Sea).

Type locality: Massawa, Eritrea, Red Sea (as defined by neotype).

Type material: Neotype: HUJ F.6708, as designated by IWATSUKI et al. (1995: 459).

Genus name: *Sciaena*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *stridens*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Korkor, Gorgor.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Sciaena stridens*; the name is binominal in both the index and text, is accompanied by a description, and is therefore available as *Sciaena stridens* Forsskål in Niebuhr, 1775; the species was treated as valid since BONNATERRE (1788: 121) and WALBAUM (1792: 317). *Perca korkor* Lacepède [ex Forsskål], 1802 (LACEPÈDE 1802: 397, 418–421; misspelled *Perca korker* on p. 397) is an unneeded new name for *Sciaena stridens* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Nemipteridae – Threadfin breams

"*Scolopsis ghanam* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "56. [SCIÆNA] n) GHANAM. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44): "SCIÆNA ... 4) GHANAN.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 50): "56. SCIÆNA GHANAM; *albida, lateribus utrinque vitta gemina, alba.*".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Type material: Syntype: ZMUC P.4782 (dry skin) (listed as holotype by ESCHMEYER 2007) (see KLAUSEWITZ & NIELSEN 1965: 19, pl. 17; MØLLER 2006).

Genus name: *Sciaena*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *ghanam*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu m'sámmer, Ghanam.

Remarks: In his draft, FORSSKÅL used the Arabic name 'Ghanam' as a substitute for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the new species as *Sciaena ghanam*. The name is binominal both in index and text, is accompanied by a diagnosis and description, and therefore would be available as *Sciaena ghanam* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Scolopsis ghanam* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 123) and WALBAUM (1792: 318). *Sciaena ghanan* of FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44) is a misspelling of *Sciaena ghanam*.

Lethrinidae – Emperors

Lethrinidae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "[61. SCIÆNA s) NEBULOSA] β) *violaceo-fasciata. Abu hamrûr.*".

FORSSKÅL in NIEBUHR (1775a: 52): "61. [SCIÆNA NEBULOSA, HAMRUR] b) *Variat*: vittis longitudinalibus obsoletis violaceis; quarum una prope abdomen rubens, lata. Arab. *Abu hamrûr.*".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): (Var. b.); (FABRICIUS in NIEBUHR): *nebulosa violaceo-fasciata*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu hamrûr.

Remarks: In his draft, FORSSKÅL listed this as variety 'b' without a scientific variety name. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) did not give a variety name in the text, but printed '*violaceo-fasciata*' as the variety name in the index. The name was accompanied by a brief diagnosis, and would be available as *Sciaena nebulosa violaceofasciata* Fabricius in Niebuhr, 1775, the authorship pending a decision of ICZN. This species is not identifiable within the family Lethrinidae.

Lethrinus sp.

FORSSKÅL in NIEBUHR (1775a: XII): "[64. SCIÆNA v) OBSOLETA] β) *lamina maxillari. Dib.*".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 53): "64. [SCIÆNA RAMAK, OBSOLETA] b) DIB (Arab.) *lamina transversa membranacea in utraque maxilla.* Dentes laterales acuti. Cæterum simillima priori: sed major 2 spitham.".

Type locality: – (Red Sea).

Type material: No types known. Material may be among ZMUC P.49350 or P.49351.

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *ramak obsoleta dib*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Dib.

Remarks: In his draft, FORSSKÅL listed this as variety 'b' without a scientific variety name. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) did not give a variety name in the index, but printed 'dib' as the variety name in the text, though explicitly stating that this is an Arabic name ('Arab.'). Though the name was accompanied by a brief diagnosis, it is not available as *Sciaena ramak obsoleta dib* Fabricius in Niebuhr, 1775, because the subspecies name consisted of two words and was therefore not trinominal (ICZN, Art. 5), and because the variety name was not meant to be a scientific name, but clearly indicated to be the Arabic name. The species was subsequently named *Sciaena Dib* by GMELIN [ex FORSSKÅL] in 1789 (GMELIN 1789: 1305), based on FORSSKÅL in NIEBUHR's (1775a) diagnosis; it would be available as *Sciaena dib* Gmelin [ex Forsskål], 1789. This species was considered as valid by WALBAUM (1792: 310), but is not identifiable within the genus *Lethrinus*. It would be recommendable to have this name suppressed by a petition to the International Commission on Zoological Nomenclature.

Lethrinus sp.

FORSSKÅL in NIEBUHR (1775a: XII): "[64. SCIÆNA v) OBSOLETA] γ) *Suli. Djard. Mork. Saka. Kersit.*".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 53): "64. [SCIÆNA RAMAK, OBSOLETA] c) Nomine tantum notæ sunt mihi sequentes: SULI: DJARD: MORK: SAKA: KERSIT.".

Type locality: – (Red Sea).

Type material: No types known. Material may be among ZMUC P.49350 or P.49351.

Genus name: *Sciaena*.

Species/subspecies name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *ramak obsoleta suli*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Suli, Djard, Mork, Saka, Kersit.

Remarks: In his draft, FORSSKÅL listed several Arabic names of this variety of *Sciaena obsoleta*, but did not assign a scientific variety name. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) used '*suli*' as the variety name in the index, but not in text. Though both index and text versions are linked together by the species code '64γ' or '64c', *Sciaena obsoleta suli* Fabricius in Niebuhr, 1775 is neither accompanied by a diagnosis nor a description, and therefore not available. It is not identifiable within the genus *Lethrinus*.

"*Lethrinus harak* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "63. [SCIÆNA] u) HARAK; pinnis rubris. *Abu m'hárrak.*".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 52): "63. SCIÆNA HARAK; *virescens, pinnis pallide rubris; macula utrinque nigra lineari infra lineam lateralem.*".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.49348 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 21; see also pl. 22) (listed as syntype by MØLLER 2006); paralectotype: ZMUC P.49349 (dry skin) (MØLLER 2006).
Genus name: *Sciaena*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *harak*.
Arabic name (Latinised, FORSSKÅL): Abu m'hárrak; (FABRICIUS in NIEBUHR): Abu m'harrak.
Remarks: In his draft, FORSSKÅL used the Arabic name "M'hárrak" or "harak" as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Sciaena harak*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and would be available as *Sciaena harak* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Lethrinus harak* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 124) and WALBAUM (1792: 312).

"*Lethrinus mahsena* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "62. [SCIÆNA] t) MAHSENA; transversim fasciata *Mobseni*. [..., Arabic name]".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 52): "62. SCIÆNA MAHSENA; *fusca, lineata, fasciis transversis nebulosis, argenteis*. Arab. *Sjöûr mohseni:* Aliis *Sööbi:* vel *Hösni: Mæhseni*. [..., Arabic name]".
Type locality: "Capta ad promontorium *Djimûm*" (Ra's Barīdī, NNW Yanbu', Saudi Arabia, 24°17'N 37°31'E).
Type material: Lectotype: ZMUC P.49346 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 21; see also pl. 21); paralectotype: ZMUC P.49347 (dry skin) (MØLLER 2006).
Genus name: *Sciaena*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *mahsena*.
Arabic names (Latinised, FORSSKÅL): Sjöûr mehseni, Sööbi, Hösni, Maehseni; (FABRICIUS in NIEBUHR): Mobseni.
Remarks: In his draft, FORSSKÅL used the Arabic name 'Maehseni' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Sciaena mahsena*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and would be available as *Sciaena mahsena* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Lethrinus mahsena* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN; it is a valid species. This species was subsequently named *Sciaena masehna* by WALBAUM (1792: 310, 715); this is not an independent species description, but a spelling error.

Lethrinus nebulosus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "61. [SCIÆNA] f) NEBULOSA. *Schaur*. [..., Arabic name]".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 52): "61. SCIÆNA NEBULOSA, HAMRUR; Ar. *Scháûr*. [..., Arabic name] Aliis *Bónkose*. [..., Arabic name]".
Type locality: – (Red Sea); – "Aliis" (Red Sea).
Type material: Syntype: ZMUC P.49345 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 21, pl. 20) (listed as holotype by MØLLER 2006 and ESCHMEYER 2007).
Genus name: *Sciaena*.
Species names (FORSSKÅL): *nebulosa*; (FABRICIUS in NIEBUHR): *nebulosa, hamrur*.
Arabic names (Latinised, FORSSKÅL): Scháûr, Bónkose; (FABRICIUS in NIEBUHR): Schaur.
Remarks: FORSSKÅL intended to describe this species as *Sciaena nebulosa*, and this is how it was named in the index on p. XII. FABRICIUS in NIEBUHR described the species on p. 52 as *Sciaena nebulosa, hamrur*; the name 'hamrur' was confused with the variety 'b', which has the Arabic name 'Abu hamrûr', a name that does not apply to the nominal form *Sciaena nebulosa*. As FABRICIUS in NIEBUHR (1775a) described two alternative names for the species, *nebulosa* or *hamrur*, he did not clearly decide how to name the species, so the version on p. 52 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '61'; the name on p. XII is thus accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Sciaena nebulosa* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 124) and WALBAUM (1792: 310).

Lethrinus obsoletus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "64. [SCIÆNA] v) OBSOLETA; flavo-violaceo-lineata *Ramak* [..., Arabic name]".
FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 52–53): "64. SCIÆNA RAMAK, OBSOLETA; *albido-virescens, lineis longitudinalibus obsoletis, violaceo-flaventibus; pinnis rubentibus*.".
Type locality: – (Red Sea).
Type material: Lectotype: ZMUC P.49352 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 21; see also pl. 23); paralectotype: ZMUC P.49353 (dry skin) (MØLLER 2006).
Genus name: *Sciaena*.
Species names (FORSSKÅL): *obsoleta*; (FABRICIUS in NIEBUHR): *ramak, obsoleta*.
Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Ramak.
Remarks: FORSSKÅL intended to describe this species as *Sciaena obsoleta*, and this is how it was named in the index on p. XII. FABRICIUS in NIEBUHR described the species on pp. 52–53 as *Sciaena ramak, obsoleta*. As FABRICIUS in NIEBUHR (1775a) described two alternative names for the species, *ramak* or *obsoleta*, he did not clearly decide how to name the species, so the version on pp. 52–53 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '64'; the name on p. XII is thus accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Sciaena obsoletus* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 124), who also acted as the first reviser of this case, and chose the name *obsoletus* as having priority over *ramak*.

Monotaxis grandoculis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "65. [SCIÆNA] w) GRANDOCULIS; cærulescens. *Abu æjn*. [..., Arabic name]".
FORSSKÅL in NIEBUHR (1775a: 53): "65. SCIÆNA GRANDOCULIS; *cærulescens: labio inferiore gibbo*.".
Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).
Genus name: *Sciaena*.
Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *grandoculis*.
Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu æjn.
Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Sciaena grandoculis*; the name is binominal in both the index and text, is accompanied by a description, and is therefore available as *Sciaena grandoculis* Forsskål in Niebuhr, 1775. The species was treated as

valid since Bonnaterre (1788: 125) and Walbaum (1792: 311–312).

Sparidae – Porgies

"Acanthopagrus berda (Forsskål in Niebuhr, 1775)"

Fabricius [ex Forsskål] in Niebuhr (1775a: XI): "24. [SPARUS] d) berda; spinis basi bulbosis. *Abu basal* vel *Nezi*. [..., Arabic name] Lohajæ.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 32–33): "24. SPARUS berda; *cinereo-albidus; squamis lateralibus singulis fascia media, transversa, fusca: spinis dorsalibus recumbentibus*.".

Type locality: "Lohajæ" (Al-Luhayya/Yemen).

Type material: Holotype: ZMUC P.50555 (see Klausewitz & Nielsen 1965: 16, pl. 6; Møller 2006).

Genus name: *Sparus*.

Species name (Forsskål): –; (Fabricius in Niebuhr): *berda*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Abu basal, Nezi, Berda.

Remarks: In his draft, Forsskål did not give a species name, but used 'berda' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr described the species as *Sparus berda*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and therefore would be available as *Sparus berda* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Acanthopagrus berda* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since Walbaum (1792: 292). Though Eschmeyer (2007) states that this was described as a new name for *Chaetodon bifasciatus* Forsskål in Niebuhr, 1775 (see below, *Acanthopagrus bifasciatus*), no evidence for this hypothesis is found in the original description.

Acanthopagrus bifasciatus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XIII): "91. [CHÆTODON] n) bifasciatus. *Rabâgi*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 64–65): "91. CHÆTODON bifasciatus; *cauda bifida, flava, fasciis duabus capitis nigris*.".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.50557 (dry skin) (see Klausewitz & Nielsen 1965: 24, pl. 35; Møller 2006).

Genus name: *Chætodon*.

Species name (Forsskål, Fabricius in Niebuhr): *bifasciatus*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Rabâgi, Rabdja, Robgi.

Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Chætodon bifasciatus*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Chaetodon bifasciatus* Forsskål in Niebuhr, 1775. The species was treated as valid by Bonnaterre (1788: 85). *Holocentrus rabaji* Lacepède [ex Forsskål], 1802 (Lacepède 1802: 724, 725) was described as a an unneeded new name for *Chaetodon bifasciatus*, and is a junior synonym.

Argyrops spinifer (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XI, part): "23. [SPARUS] c) spinifer; quinque-filaris. *Naddjar*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 32): "23. SPARUS spinifer; *spinis dorsalibus recumbentibus, mediis quinque filiformibus, longioribus*.".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Sparus*.

Species name (Forsskål, Fabricius in Niebuhr): *spinifer*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Naddjar, Quidjâdj, Djidjadj el báhr.

Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Sparus spinifer*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Sparus spinifer* Forsskål in Niebuhr, 1775; it is in part a valid species (considered as valid since Walbaum 1792: 299–300), now named *Argyrops spinifer* (Forsskål in Niebuhr, 1775). Turkish and Egyptian records of *Sparus spinifer* by Forsskål in Niebuhr (1775a: XI, part) are based on *Pagrus* sp. (see below). A neotype needs to be selected for this species in order to stabilise the usage as *Argyrops spinifer*.

Boops boops (Linnaeus, 1758)

Forsskål in Niebuhr (1775a: XV): "22. [SPARUS] k) *cantharus*. Oblongus, vertice rugoso. Βῶπα. Turc. *Vupa*. Arab. *Måsi*. An idem cum *Sp. boope*?. Vel. Γῶπα. Smirnensium?".

Localities: "Smirna?" (İzmir/Turkey); "Alexandria" (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Material: ZMUC P.50552 (dry skin) (see Klausewitz & Nielsen 1965: 16).

Genus name: *Sparus*.

Actual Turkish names: Kupez, lopa (Fricke et al. 2007: 86).

Remarks: This is not an independent new species description, but a misidentification of *Sparus cantharus* (non Linnaeus, 1758); the record is based on *Boops boops* (Linnaeus, 1758). This species is common in the Marmara Sea near İstanbul and the Aegean Sea near İzmir in Turkey; it was probably collected by Forsskål using a chartered fishing vessel at Constantinople/İstanbul. One of the actual Turkish names of the species is 'lopa' (Fricke et al. 2007: 86), which resembles the 'vupa' recorded by Forsskål.

Boops boops (Linnaeus, 1758)

Forsskål [ex Anonymus] in Niebuhr (1775a: XVIII): "[Sparus] *boops*.".

Locality: "Melita" (La Valletta/Malta).

Crenidens crenidens (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XV): "19. [SPARUS] g) crenidens. Djiddæ *Rasan*. Sués *Boreis* [..., Arabic name] vel *Ersan*. *Opercula* inermia. ...".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Sués" (As-Suways/Egypt).

Type material: Syntype: ZMUC P.50551 (probably from Jeddah) (see Klausewitz & Nielsen 1965: 16, pl. 5) (listed as holotype by Møller 2006).

Genus name: *Sparus*.

Species name (Forsskål, Fabricius in Niebuhr): *crenidens*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Rasan, Boreis, Ersan.

Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Sparus crenidens*; the name is binominal in both the index and text, is accompanied by a diagnosis, and is therefore available; it is a valid species, now named *Crenidens crenidens* (Forsskål in Niebuhr, 1775). The species was named *Sparus crenideus* by Walbaum (1792: 303, 716); this is not an independent species description, but a spelling error. It was subsequently described as *Crenidens forskalii* Valenciennes in Cuvier & Valenciennes, 1830 (Valenciennes in Cuvier & Valenciennes 1830: 378), which is a junior synonym of *Crenidens crenidens*.

?Cheimerius nufar (Valenciennes in Cuvier & Valenciennes, 1830)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XVII): "55. [?*Sciæna*] NAQUA; piscis maris rubri obscurus; (an *Sciæna* 48.?) …".

Locality: – (Red Sea).

Remarks: FORSSKÅL in NIEBUHR (1775a) used the Arabic name 'naqua' as a substitute for a scientific name possibly to be selected for this species, doubtfully arranged in the genus *Sciaena*, and possibly thought conspecific with *Sciaena gibba* (species code '48'). FABRICIUS in NIEBUHR (1775a) used (*Sciaena?*) *naqua* to name a species which was insufficiently diagnosed, not meant to be a new species with certainty, and therefore not available as *Sciaena naqua* Fabricius in Niebuhr, 1775. The record was probably based on the sparid fish *Cheimerius nufar* (Valenciennes in Cuvier & Valenciennes, 1830). The name *Naqua* was erroneously interpreted by ESCHMEYER (2007) to be a subgenus of *Sciaena*, and considered a species of *Lutjanus*.

Dentex sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SPARUS] *dentex*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Dentici".

Remarks: The record of the Linnaean species name *Sparus dentex* from Malta cannot be assigned to species level; the record could have been based on either *Dentex dentex* (Linnaeus, 1758), *Dentex gibbosus* (Rafinesque-Schmaltz, 1810), *Dentex macrophthalmus* (Bloch, 1791) or *Dentex maroccanus* Valenciennes in Cuvier & Valenciennes, 1830 (actual vernacular Maltese name "Denci"; Anonymus 2007b).

Diplodus annularis (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "17. SPARUS e) *annularis*. Σπάρος. Turc. *Smarid*. Arab. *Háros*. Corpus ovale. Ad caudam non ocellus, sed macula nigra. P. V. flava.".

Localities: "Turc." (Turkey); "Alexandria" (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Actual Turkish names: İsparoz, İspari (FRICKE et al. 2007: 87).

Remarks: This is a record of the Linnaean species *Sparus annularis*; its currently used name is *Diplodus annularis* (Linnaeus, 1758). The species frequently occurs in the Marmara Sea near İstanbul and the Aegean Sea near İzmir in Turkey.

Diplodus annularis (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SPARUS] *sparus*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il Spargu".

Remarks: *Sparus sparus* Forsskål [ex Anonymus] in Niebuhr, 1775 is a name only (nomen nudum), as it was listed with neither a diagnosis nor an indication. The name is not included in ESCHMEYER (2007). According to the Maltese name, the record has been based on *Diplodus annularis* (Linnaeus, 1758) (actual vernacular Maltese name "Sparlu"; Anonymus 2007b).

Diplodus sargus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "20. [SPARUS] h) *sargus*. Ασκάδαρος.".

Locality: – (Turkey).

Remarks: This is a record of the Linnaean species *Sparus sargus*; its currently used name is *Diplodus sargus* (Linnaeus, 1758), with the actual Turkish name 'Sargoz' (FRICKE et al. 2007: 87). The species frequently occurs in the Marmara Sea near İstanbul and the Aegean Sea near İzmir in Turkey.

Lithognathus mormyrus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "14. [SPARUS] b) *mormyrus*. Μύρμυρ.".

Locality: – (Turkey?).

Remarks: This is a record of the Linnaean species *Sparus mormyrus*; its currently used name is *Lithognathus mormyrus* (Linnaeus, 1758), with the actual Turkish name 'Mirmir' (FRICKE et al. 2007: 87). The species frequently occurs in the Marmara Sea near İstanbul and the Aegean Sea near İzmir in Turkey.

Oblada melanura (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "18. [SPARUS] f) *melanurus*. Μελανύρα. Arab. *Kabli* vel *Schargûsch*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SPARUS] *melanurus*.".

Localities: – (Turkey?); "Alexandria" (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea); "Melita" (La Valletta/Malta).

Remarks: These records are based on the Linnaean species *Sparus melanurus*; its currently used name is *Oblada melanura* (Linnaeus, 1758). This species frequently occurs in the Marmara Sea near İstanbul and the Aegean Sea near İzmir in Turkey (FRICKE et al. 2007: 88), and in other parts of the Mediterranean Sea.

Pagellus erythrinus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SPARUS] *erythrinus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Pagella".

Remarks: This record under the Linnaean name *Sparus erythrinus* from Malta has actually been based on *Pagellus erythrinus* (Linnaeus, 1758), according to the Maltese name (actual vernacular Maltese name "Pagella"; Anonymus 2007b).

Pagrus sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SPARUS] *pagrus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Pagru".

Remarks: This record under the Linnaean name *Sparus pagrus* from Malta cannot be assigned to species level; the record could have been based on either *Pagrus auriga* Valenciennes, 1843 or *Pagrus caeruleostictus* (Valenciennes in Cuvier & Valenciennes, 1830), both bearing the actual vernacular Maltese name "Pagru" (Anonymus 2007b).

Pagrus sp.

FORSSKÅL in NIEBUHR (1775a: XI, part): "23. SPARUS c) SPINIFER; quinque-filaris. Constantinopoli *Merdjan*.".

Type localities: "Constantinopoli" (İstanbul/Turkey); "DAMIATÆ" (Dumyāt/Egypt); (part).

Remarks: *Sparus spinifer* Forsskål in Niebuhr, 1775 was in part described from Constantinople/İstanbul, Turkey; according to the presence of filaments in the dorsal fin, and the Turkish name (actual Turkish name 'Mercan'), it could be based on either of the two species of *Pagrus* occurring in the Marmara Sea and Bosporus in the area (FRICKE et al. 2007: 88): *Pagrus auriga* Valenciennes, 1843 (Çizgili mercan), or *Pagrus caeruleostictus* (Valenciennes in Cuvier & Valenciennes, 1830) (Antenli mercan). Both species are today no longer known from Marmara Sea, but do occur in the Aegean Sea. Red Sea materials of *Sparus spinifer* belong to a valid species, *Argyrops spinifer* (Forsskål in Niebuhr, 1775). A neotype needs to be selected for this species in order to fix the usage as *Argyrops spinifer*.

Pagrus caeruleostictus (Valenciennes in Cuvier & Valenciennes, 1830)

FORSSKÅL in NIEBUHR (1775a: XV): "15. [SPARUS] c) *pagrus*. Μερχιανι. Turc. *Mertsan*. nomen Persicum. Venter a capite ad anum fere rectus; unde habitus Triglæ.".

Locality: "Turc." (İzmir/Turkey).

Actual Turkish name: Antenli mercan (FRICKE et al. 2007: 88).

Remarks: This is a misidentification of the species *Sparus pagrus* (non Linnaeus, 1758); according to the Turkish name and the diagnosis, the record is based on *Pagrus caeruleostictus* (Valenciennes in Cuvier & Valenciennes, 1830), a species which is regularly found in the Aegean Sea near İzmir/Turkey, but not in the Marmara Sea near İstanbul. The Turkish name of the co-occurring *Pagrus pagrus* (Linnaeus, 1758) is 'Fangri' (FRICKE et al. 2007: 88).

"*Rhabdosargus haffara* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "25. [SPARUS] e) HAFFARA; lineis flavis 14. *Haffâra*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 33): "25. SPARUS HAFFARA. DESCR. Facies Mormyri. Fasciæ transversæ nullæ. ...".

Type locality: – (Red Sea).

Genus name: *Sparus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *haffara*.

Arabic name (Latinised, FORSSKÅL): Haffâra; (FABRICIUS in NIEBUHR): Haffâra.

Remarks: In his draft, FORSSKÅL used 'Haffara' as a substitute name for a Latin name to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described it as a new species *Sparus haffara*. The name is binominal in both the index and text, and accompanied by a description; it would therefore be valid as *Sparus haffara* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Rhabdosargus haffara* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN, and was treated as valid since BONNATERRE (1788: 101) and WALBAUM (1792: 203).

Rhabdosargus sarba (Gmelin [ex Forsskål], 1789)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "22. [SPARUS] b) SARBA; argenteus. *Arid*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 31–32): "22. SPARUS SARBA; *ovato-oblongus, argenteus: vittis obsoletis plurimis: linea aurea utrinque juxta pinnas ventrales flavas:* an *Salpa Linn.?*".

Type localities: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); "Suénsium" (As-Suways/Egypt).

Type material: Lectotype: ZMUC P.50553 (said to be a holotype by ESCHMEYER 2007) (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 16, see also pls. 5–6); paralectotype: ZMUC P.50554 (dry skin) (MØLLER 2006).

Genus name: *Sparus*.

Species names (FORSSKÅL): – (*argenteus*); (FABRICIUS in NIEBUHR): *sarba* or *salpa*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Arid, Kosar, Sarba.

Remarks: FORSSKÅL was not sure if this was a new species or a record of *Sparus salpa* Linnaeus, 1758 from the Red Sea; he used the Arabic name 'sarba' as a substitute for a Latin name eventually to be selected, if this turned out to be a new species. FABRICIUS in NIEBUHR mentioned in the text that this is either a new species *Sparus sarba*, or *Sparus salpa*. As neither FORSSKÅL nor FABRICIUS were sure of the identity of the new species, but used two alternative names, the name *Sparus sarba* Fabricius [ex Forsskål] in Niebuhr, 1775 is not available. The first available version of the name is *Sparus sarba* Gmelin [ex Forsskål], 1789 (GMELIN 1789: 1275). The species was considered as valid since WALBAUM (1792: 294–205).

Sarpa salpa (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XV): "SPARUS a) *salpa*. Σάλπα.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[SPARUS] *salpa*.".

Localities: – (İstanbul or İzmir, Turkey); "Melita" (La Valletta/Malta). Local Maltese name: "I Scilpa".

Sparus aurata Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "SPARUS *auratus*.".

Locality: "Melita" (La Valletta/Malta).

Spondyliosoma cantharus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "16. [SPARUS] d) Μαυρόψαρο: lineatus, ovalis; cauda bifida; vertice lævi; corpore albo, lineis flavicantibus interceptis in medio latere. ...".

Type locality: – (İstanbul or İzmir, Turkey).

Genus name: *Sparus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): Μαυρόψαρο.

Remarks: While FORSSKÅL used the Greek name 'Μαυρόψαρο' as a substitute for a Latin name possibly to be selected, FABRICIUS in NIEBUHR took the name to describe it as a new species. However, as the name is not in Latin characters, it is not available. *Sparus Μαυρόψαρο* is an unavailable junior synonym of *Sparus cantharus* Linnaeus, 1758; its currently used name is *Spondyliosoma cantharus* (Linnaeus, 1758). This species was subsequently described as *Sparus mauropsarus* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 301) and *Sparus mauropsaro* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 279), based on FORSSKÅL's *Sparus* Μαυρόψαρο; *Sparus mauropsaro* is a junior synonym of *Spondyliosoma cantharus* (Linnaeus, 1758). ESCHMEYER (2007) erroneously gave the type locality of *Sparus mauropsaro* Bloch & Schneider as 'Red Sea', but it is western Turkey. PARENTI in ESCHMEYER (2007), also erroneously, gave the identity of *Sparus mauropsarus* Walbaum as *Rhabdosargus sarba* (non Gmelin [ex Forsskål], 1789).

Spondyliosoma cantharus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "23. [SPARUS] l) *strongilus*. Στρόγγιλο. Turc. *Strongíl*. Arab. *Guegára*. Oblongus, sublineatus, ...".

Type localities: "Turc." (Turkey); "Alexandria" (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Genus name: *Sparus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *strongilus*.

Remarks: While FORSSKÅL, in his draft, used the Greek name 'Στρόγγιλο' as a substitute for a Latin name possibly to be selected, FABRICIUS in NIEBUHR used the *Sparus strongilus* to describe it as a new species. The name is binominal and accompanied by a diagnosis; it would therefore be available as *Sparus strongilus* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The name was subsequently spelled *Sparus strongylus* by BLOCH & SCHNEIDER (1801: 285). *Sparus strongilus* Fabricius [ex Forsskål] in Niebuhr, 1775 is a junior synonym of *Sparus cantharus* Linnaeus, 1758.

Spondyliosoma cantharus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SPARUS] *cantharus*.".

Locality: "Melita" (La Valletta/Malta).

Centracanthidae – Picarel porgies

Spicara maena (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "21. [SPARUS] i) *mæna*. Σερώλα.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SPARUS] *mænas*.".

Localities: – (Turkey?); "Melita" (La Valletta/Malta). Local Maltese name: "Il Minnula".

Remarks: Both records are based on the Linnaean species *Sparus maena*, which is a valid species with the currently used name *Spicara maena* (Linnaeus, 1758). The species frequently occurs at İstanbul and İzmir in Turkey; the specimen which forms the basis of the record on p. XV was probably collected by FORSSKÅL with the chartered fishing vessel at Constantinople/İstanbul, Turkey. The species name '*maenas*' is a spelling error for '*maena*', not an independent naming of the species.

Spicara smaris (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "SPARUS *smaris*.".

Locality: "Melita" (La Valletta/Malta).

Sciaenidae – Drums

Sciaenidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SCIÆNA] *umbrina*.".

Type locality: "Melita" (La Valletta/Malta).

Remarks: This is a name only (nomen nudum), as it was accompanied by neither a diagnosis, nor a description or indication. Therefore, the name is not available as *Sciaena umbrina* Forsskål in Niebuhr, 1775. The species is unidentifiable within the family Sciaenidae.

Sciaena umbra Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "SCIÆNA *umbra*.".

Locality: "Melita" (La Valletta/Malta).

Mullidae – Goatfishes

Mullus surmuletus Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XVI): "31. MULLUS *barbatus*. Βαρβῦνι. Turc. *Tekir*. Esca vulgaris & fastidita Constantinopoli; Romanis olim ichthyophaga & pretiosa luxuria.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "MULLUS *surmuletus*.".

Localities: "Constantinopoli" (İstanbul/Turkey); "Melita" (La Valletta/Malta).

Actual Turkish name: Tekir (FRICKE et al. 2007: 90).

Remarks: The Turkish record is a misidentification of the species *Mullus barbatus* (non Linnaeus, 1758); according to the Turkish name, the record is based on *Mullus surmuletus* Linnaeus, 1758, a species which is regularly found in shallow water around İstanbul. The specimen recorded by FORSSKÅL was probably collected by the fishing vessel which he chartered in Constantinople/İstanbul. *Mullus barbatus* has the actual Turkish name 'Barbun' (FRICKE et al. 2007: 90). From Malta, *Mullus surmuletus* is given as a name only, so we cannot be sure if it was correctly identified.

Parupeneus forsskali (Fourmanoir & Guézé [ex Forsskål], 1976)

FORSSKÅL in NIEBUHR (1775a: X): "19. MULLUS a) AURIFLAMMA; vittis aureis. *Ambîr*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 30): "19. MULLUS AURIFLAMMA: *cirrhis duobus albis, vitta utrinque fulva; dorso fusco æneo: caudæ pinna flava, immaculata*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.49343 (see KLAUSEWITZ & NIELSEN 1965: 14–15, pl. 4; MØLLER 2006).

Genus name: *Mullus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *auriflamma*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Ambîr.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Mullus auriflamma*; as the name would have been available and might have threatened its commonly used junior synonym *Upeneus vanicolensis* Valenciennes in Cuvier & Valenciennes, 1831, *Mullus auriflamma* Forsskål, 1775 was placed on Official Index of Rejected Names in Opinion 846 (Anonymus 1968). *Pseudupeneus forsskali* Fourmanoir & Guézé, 1976 (FOURMANOIR & GUÉZÉ 1976: 45) was described as a replacement name for *Mullus auriflamma*; the species has the currently used name *Parupeneus forsskali* (Fourmanoir & Guézé [ex Forsskål], 1976). *Mullus auriflamma* was erroneously placed in the synonymy of *Mulloidichthys vanicolensis* (Valenciennes in Cuvier & Valenciennes, 1831) by authors, including RANDALL (2005: 293) and ESCHMEYER (2007).

Upeneus vittatus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "20. [MULLUS] b) VITTATUS; quinque-fasciatus. *Abu dagn*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 31): "20. MULLUS VITTATUS; *cirrhis geminis: corporis vittis utrinque duabus fuscis, tribus flavis: pinna caudæ oblique fuscata*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.49344 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 15–16, pl. 4; MØLLER 2006).

Genus name: *Mullus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *vittatus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu dagn.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR (1775a) as *Mullus vittatus*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available. The species was treated as valid since BONNATERRE (1788: 144) and WALBAUM (1792: 620).

Monodactylidae – Moonfishes

Monodactylus argenteus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XII): "78. [SCOMBER] k) RHOMBEUS; *Abu gurr*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 58): "78. SCOMBER RHOMBEUS: *pinnis ventralibus uni-radiatis*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.50556 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 23, pl. 29; MØLLER 2006).

Genus name: *Scomber*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *rhombeus*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu gurr, Abu tabak.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scomber rhombeus*; the name is binominal in both text and index, is accompanied by a diagnosis and description, and therefore available as *Scomber rhombeus* Forsskål in Niebuhr, 1775. The name was considered as valid by WALBAUM (1792: 221–222). It is, however, a junior synonym of *Monodactylus argenteus* (Linnaeus, 1758).

Kyphosidae – Sea chubs

Kyphosus cinerascens (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "66. [SCIÆNA] x) CINERASCENS. *Táhmel.* [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 53): "66. SCIÆNA CINERASCENS, TAHMEL; *cinereo-virescens, lineis longitudinalibus flavis.*".

Type locality: – (Red Sea).

Genus name: *Sciaena*.

Species names (FORSSKÅL): *cinerascens*; (FABRICIUS in NIEBUHR): *cinerascens*, *tahmel*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Táhmel.

Remarks: FORSSKÅL intended to describe this species as *Sciaena cinerascens*, and this is how it was named in the index on p. XII. FABRICIUS in NIEBUHR described the species on p. 53 as *Sciaena cinerascens*, *tahmel*. As FABRICIUS in NIEBUHR (1775a) described two alternative names for the species, *cinerascens* or *tahmel*, he did not clearly decide how to name the species, so the version on p. 53 is not available (ICZN, Art. 11.5). Both versions, however, are linked together by the species code '66'; the name on p. XII is thus accompanied by a diagnosis and description, and is available by indication (ICZN, Art. 12.2.2) as *Sciaena cinerascens* Forsskål in Niebuhr, 1775. The species was treated as valid since BONNATERRE (1788: 125, *Sciaena cinerascens*) and WALBAUM (1792: 312). RÜPPELL (1837: 35) treated the second of FORSSKÅL in NIEBUHR's names for this species, 'tahmel', as valid, and named it *Pimelepterus tahmel*; *Pimelepterus tahmel* Rüppell, 1837 is a junior synonym of *Sciaena cinerascens* Forsskål in Niebuhr, 1775.

Chaetodontidae – Butterflyfishes

Chaetodon auriga Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: XIII): "81. CHÆTODON c) AURIGA; radio quinto filari. *Mókti.* [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 60): "81. CHÆTODON AURIGA; *albidus, oblique fasciatus; radio pinnæ dorsalis quinto in filum producto.*".

Type localities: "Djiddæ" (Jeddah, Juddah/Saudi Arabia); "Lohajæ" (Al-Luhayya/Yemen).

Type material: Holotype: ZMUC P.52401 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 23, pl. 32; MØLLER 2006).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *auriga*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Mókti, Tabak el kuss, Schaûsch.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon auriga*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Chaetodon auriga* Forsskål in Niebuhr, 1775. The species is considered as valid since WALBAUM (1792: 422).

Chaetodon fasciatus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: XII): "80. [CHÆTODON] b) FASCIATUS; flavus. *Tabak el kûs.*".

FORSSKÅL in NIEBUHR (1775a: 59–60): "80. CHÆTODON FASCIATUS; *flavus; fascia oculari nigra: supra nucham, alba: per latera, ferrugineo-fusca.*".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.52400 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 23, pl. 31; MØLLER 2006).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *fasciatus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Tábak el kûs.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon fasciatus*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Chaetodon fasciatus* Forsskål in Niebuhr, 1775. The species was considered as valid since RÜPPELL (1852: 9). *Chaetodon tabak* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 421) and *Chaetodon flavus* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 225–226) were described as unneeded new names for *Chaetodon fasciatus* Forsskål in Niebuhr, 1775; they are junior synonyms.

Chaetodon mesoleucos Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: XIII): "83. [CHÆTODON] e) MESOLEUCOS; hinc albus, inde fuscus. *Hadjan*".

FORSSKÅL in NIEBUHR (1775a: 61): "83. CHÆTODON MESOLEUCOS; *parte anteriore albus, posteriore fuscus, fasciis nigris.*".

Type locality: "MOCHHÆ" (Al-Mukhā/Yemen).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *mesoleucos*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Hadjan.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon mesoleucos*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Chaetodon mesoleucos* Forsskål in Niebuhr, 1775. The species is considered as valid since WALBAUM (1792: 411, *Chaetodon mesoleucus* sensu FORSSKÅL, spelling error). This is one of the last fish species discovered by P. S. FORSSKÅL in May, June or July 1763. *Chaetodon hadjan* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 227) was described as an unneeded new name for *Chaetodon mesoleucos* Forsskål in Niebuhr, 1775, to distinguish this species from *Chaetodon mesoleucus* Bloch, 1787 [BLOCH 1787: 117, pl. 216, fig. 2; currently used name *Chaetodontoplus mesoleucus* (Bloch, 1787), Pomacanthidae]; *Chaetodon hadjan* is a junior synonym of *Chaetodon mesoleucos* Forsskål in Niebuhr, 1775. The name *Chaetodon mesoleucus arabicus* Walbaum [ex Forsskål], 1792 was described as a 'varietas aut alia species' (variety or other species) by WALBAUM (1792: 411); it is accompanied by a description, is available, but a junior synonym of *Chaetodon mesoleucos* Forsskål in Niebuhr, 1775.

Chaetodon pictus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: XIII): "92. [CHÆTODON] o) PICTUS; albidus, violaceo-lineatus.".

FORSSKÅL in NIEBUHR (1775a: 65): "92. CHÆTODON PICTUS; *albidus, lineis obliquis violaceis, fascia nigra oculorum & caudæ.*".

Type locality: "*Mochhæ*" (Al-Mukhā/Yemen).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *pictus*.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon pictus* the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Chaetodon pictus* Forsskål in Niebuhr, 1775. The species is considered as valid since WALBAUM (1792: 422–423). This is one of the last fish species discovered by P. S. FORSSKÅL in May, June or July 1763.

Pomacanthidae – Angelfishes

"*Pomacanthus asfur* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "84. [CHÆTODON] f) ASFUR; fascia lunari. *Asfûr*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 61): "84. CHÆTODON ASFUR; *niger; fascia transversa, lunari-cuneata flava*.".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen).

Genus name: *Chætodon*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *asfur*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Tabak el herr, Asfûr.

Remarks: In his draft, FORSSKÅL used the Arabic name 'asfur' as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Chætodon asfur*; the name is binominal in both text and index, is accompanied by a diagnosis and description, and therefore would be available as *Chaetodon asfur* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Pomacanthus asfur* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was treated as valid since BONNATERRE (1788: 88–89) and WALBAUM (1792: 406).

Pomacanthus maculosus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XIII): "85. [CHÆTODON] g) MACULOSUS; cinereo-cæruleus. *Arusa*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 62): "85. CHÆTODON MACULOSUS, ARUSA; *cinereus, maculis transversis cæruleis: operculis anterioribus uni-spinosis*.".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen).

Type material: Holotype: ZMUC P.52402 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 23–24, pl. 33; MØLLER 2006).

Genus name: *Chætodon*.

Species names (FORSSKÅL): *maculosus*; (FABRICIUS in NIEBUHR): *maculosus*, *arusa*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Arusa, Aruset el báhr.

Remarks: FORSSKÅL intented to describe this species as *Chætodon maculosus*, and this is how it is named in the index on p. XIII. FABRICIUS in NIEBUHR described the species on p. 62 as *Chaetodon maculosus, arusa*; they did not decide how to name the species, either *maculosus* or *arusa*, and therefore the version on p. 62 is not available (ICZN, Art. 11.5). The version on p. XIII is linked by the species code '85' to the diagnosis and description on p. 62; it is therefore available by indication (ICZN, Art. 12.2.2) as *Chaetodon maculosus* Forsskål in Niebuhr, 1775. The species was considered as valid since WALBAUM (1792: 415–416). It was subsequently re-named *Chaetodon arusa* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 89), which is a junior synonym, and later described with an erroneous spelling *Holacanthus aruset* by LACEPÈDE (1802: 528, 535); the latter name is not an independent species description, but a spelling error. The name *Chaetodon arusa* was erroneously considered by authors to be a synonym of *Pomacanthus asfur* (see ESCHMEYER 2007).

Pomacanthus maculosus (Forsskål in Niebuhr, 1775)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "[84. CHÆTODON f) ASFUR] β) *caerulescens. Hæddaja*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 61): "84. [CHÆTODON ASFUR] b) *Varietas* visa *Mochhæ: cærulescens; lituris & fasciis obliquis; lineolis violaceis: P. A. breviore P. C.*".

Type locality: "MOCHHÆ" (Al-Mukhā/Yemen).

Genus name: *Chætodon*.

Species/subspecies name (FORSSKÅL): *asfur caerulescens*; (FABRICIUS in NIEBUHR): –.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Hæddaja.

Remarks: FORSSKÅL used the Latin name 'caerulescens' as a variety/subspecies of *Chaetodon asfur*. Though FABRICIUS in NIEBUHR only mentioned it as variety β of *Chætodon asfur*, both versions are linked together by the code '84b'; as FORSSKÅL's version is trinominal as *Chaetodon asfur caerulescens*, and FABRICIUS's version is accompanied by a diagnosis, the name is considered to be available by indication (ICZN, Art. 12.2.2) as *Chaetodon asfur caerulescens* Forsskål in Niebuhr, 1775. Though ESCHMEYER (2007) considers that based on type style in adjacent entries, this name was not proposed as a scientific name, the linking together of index and text versions is justified and recognisable by the species code '84b' (like in other FORSSKÅL species), and thus makes the name available. This is the juvenile of *Pomacanthus maculosus* (Forsskål in Niebuhr, 1775), which was described in the same paper. GMELIN (1789: 1267) was the first to consider *Chaetodon maculosus* Forsskål in Niebuhr, 1775 as a valid species, while he listed *Chaetodon caerulescens* in the synonymy of *Chaetodon asfur*. This usage was followed henceforth. I therefore consider the name *Chaetodon maculosus* Forsskål in Niebuhr, 1775 as having priority over *Chaetodon asfur caerulescens* Forsskål in Niebuhr, 1775. *Pomacanthus maculosus* (Forsskål in Niebuhr, 1775) is the valid name of the species. RÜPPELL's (1830: 133) *Holacanthus caerulescens* is not an independent description, but based on *Chaetodon asfur caerulescens* Forsskål in Niebuhr, 1775. – *Chaetodon asfur amarus* Bloch & Schneider [ex Forsskål], 1801 (BLOCH & SCHNEIDER 1801: 220) and *Holacanthus haddaja* Cuvier in Cuvier & Valencienes, 1831 (CUVIER in CUVIER & VALENCIENNES 1831: 175) are new names for *Chaetodon asfur caerulescens* Forsskål in Niebuhr, 1775, and additional junior synonyms of *Pomacanthus maculosus* (Forsskål in Niebuhr, 1775).

Terapontidae – Grunters

"*Terapon jarbua* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XII): "57. [SCIÆNA] o) JARBUA; fasciis circinatis. *Djarbua*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44): "SCIÆNA ... 5) DJABUB. Dentes maxillares unius seriei majores, remoti, a medio decrescentes ...".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 50): "57. SCIÆNA JARBUA; Arab. DJIDDÆ *Djarbua*. SUES *Djabûb* [..., Arabic name] vel *Djabul* vel *Gabub*.".

Type localities: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia); "SUES" (As-Suways/Egypt).

Type material: Lectotype: ZMUC P.43571 (dry skin), as designated by KLAUSEWITZ & NIELSEN (1965: 20; see also

pls. 17–18); paralectotype: ZMUC P.43572 (dry skin) (listed as syntype by Møller 2006). Another Forsskål specimen and possible paralectotype (ZMUC P.43573) is based on *Pelates quadrilineatus* (Bloch, 1790).

Genus name: *Sciaena*.

Species name (Forsskål): –; (Fabricius in Niebuhr): *jarbua*.

Arabic names (Latinised, Forsskål, Fabricius in Niebuhr): Djarbua, Djabûb, Djabul, Gabub.

Remarks: In his draft, Forsskål used the Arabic name 'Djarbua' as a substitute for a Latin name to be selected, and did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr named *Sciaena jarbua* as a new species; the name is binominal in both the index and text; the name was accompanied by a description, and therefore would be available as *Sciaena jarbua* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Terapon jarbua* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species name was treated as valid since Bonnaterre (1788: 123) and Walbaum (1792: 318). *Grammistes annularis* Bloch & Schneider [ex Forsskål], 1801 (Bloch & Schneider 1801: 188) is a new name for *Sciaena jarbua*, and a junior synonym. "(*Sciaena*) *djabub* Forsskål, 1775" {would be (*Sciaena*) *djabub* Fabricius [ex Forsskål], 1775} is another name for this species, out of the version on p. 44 (the name was not mentioned by Eschmeyer 2007); it is binominal, accompanied by a diagnosis, available, and an unused synonym of "*Sciaena jarbua* Forsskål in Niebuhr, 1775". I hereby act as the first reviser of this case to select *Sciaena jarbua* as the senior synonym.

Pomacentridae – Damselfishes

Pomacentridae, indet.

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII): "[93. CHÆTODON p) *abu dafur*] β) *Jabûd*. [..., Arabic name]".

Fabricius [ex Forsskål] in Niebuhr (1775a: 65): "93. [CHÆTODON abu dafur] b) jahûd. [..., Arabic name] an Chæt.? pedalis long. Hamo venatur: caro inutilis.".

Type locality: – (Red Sea).

Genus name: *Chætodon*.

Species/subspecies name (Forsskål): –; (Fabricius in Niebuhr): *abu dafur jabûd* or *jahûd*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Jahûd.

Remarks: Forsskål used the Arabic name 'jahud' as a substitute for a scientific name possibly to be designated for this variety/subspecies *Chætodon* sp. (with 'abu dafur' as another substitute for the species name). Fabricius in Niebuhr (1775a) named *Chætodon abu dafur Jabûd* in the index and *Chaetodon abu dafur jahûd* in the text. The first version of the subspecies name, *jabud*, is regarded as a spelling error. As the species name consists of two words, it is not considered binominal; therefore a variety described under a non-binominal name is not considered as available as *Chaetodon abu dafur jahud* Fabricius [ex Forsskål] in Niebuhr, 1775 (ICZN, Art. 5). The taxon is unidentified within the family Pomacentridae.

"*Abudefduf* Forsskål in Niebuhr, 1775"

Fabricius [ex Forsskål] in Niebuhr (1775a: 59): "CHÆTODON ... b) Abu-defduf: dentibus maxillaribus unius seriei, filiformibus, contiguis, submobilibus, obtusis: dentibus faucium nullis: annulo subtus circa oculos. P. Br. rad. 5. Spinæ P. A. 2.".

Type species: *Chaetodon sordidus* Forsskål in Niebuhr, 1775 (original designation).

Remarks: In his draft, Forsskål used the Arabic name 'Abudefduf' as a substitute for a scientific name possibly to be designated for this new subgenus of *Chætodon*. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) named *Abudefduf* as a new subgenus under the name *Chaetodon*, and provided a diagnosis. Though the diagnosis is not very detailed, the genus-group name would be considered as available by indication through assigning the type species, linked with the description of *Chaetodon sordidus*/Abu defdûf (ICZN, Art. 12.2.5), as *Abudefduf* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The type species was given by Eschmeyer (2007) as *Abudefduf sordidus* (Forsskål in Niebuhr, 1775), which is inferred from the usage of the vernacular name of that species in the original description, and is definitely the species which was used by Forsskål for the diagnosis.

Abudefduf bengalensis (Bloch, 1787)

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII): "[93. CHÆTODON p) *abu dafur*] γ) *Hanni*.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 65): "93. [CHÆTODON abu dafur] c) hanni: rostrum obtusum: dentes rigidi: molares obtusi plurium serierum: fasciæ 5, alternæ latiores: radii D. 3, 4, 5, inermes, longiores.".

Type locality: – (Red Sea).

Genus name: *Chætodon*.

Species/subspecies name (Forsskål): –; (Fabricius in Niebuhr): *abu dafur hanni*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Hanni.

Remarks: Forsskål used the Arabic name 'hanni' as a substitute for a scientific name possibly to be designated for the species *Chætodon* sp. (with 'abu dafur' as another substitute for the species name. Fabricius in Niebuhr (1775a) named *Chætodon abu dafur hanni* in both the index and text. As the species name consists of two words, it is not considered binominal; therefore a variety described under a non-binominal name is not considered as available as *Chaetodon abu dafur hanni* Fabricius [ex Forsskål] in Niebuhr, 1775 (ICZN, Art. 5). The species is identical with *Abudefduf bengalensis* (Bloch, 1787), according to Dor (1984: 179).

Abudefduf sordidus (Forsskål in Niebuhr, 1775)

Forsskål in Niebuhr (1775a: XIII): "87. [CHÆTODON] i) sordidus; fusco-cinereus. *Abu defdûf*. [..., Arabic name]".

Forsskål in Niebuhr (1775a: 62–63): "87. CHÆTODON sordidus; *fusco-cinereus, ovatus, fasciis transversis obsoletis, quatuor*.".

Type locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.56264 (dry skin) (see Klausewitz & Nielsen 1965: 24, pl. 34; Møller 2006).

Genus name: *Chætodon*.

Species name (Forsskål, Fabricius in Niebuhr): *sordidus*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Abu defdûf.

Remarks: Forsskål intended to describe this species as *Chætodon sordidus*, and this is how Fabricius in Niebuhr (1775a) named it in both the index and text. The name is binominal in both versions, accompanied by a diagnosis and description, and is therefore available as *Chaetodon sordidus* Forsskål in Niebuhr, 1775. The species was treated as valid as *Chaetodon sordidus* since Bonnaterre (1788: 90) and Walbaum (1792: 435–436).

Abudefduf vaigiensis (Quoy & Gaimard, 1825)

FORSSKÅL in NIEBUHR (1775a: XIII): "86. [CHÆTODON] h) SAXATILIS. *Gargut*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 62): "86. CHÆTODON SAXATILIS: *albidus; fasciis transversis quinque nigris*. (LINN.)".

Locality: – (Red Sea).

Material: ZMUC P.56261–56263 (3 dry skins) (see KLAUSEWITZ & NIELSEN 1965: 24).

Remarks: This is not a new species description, but a redescription of the species *Chaetodon saxatilis* (non Linnaeus, 1758). The species was misidentified; the record is based on *Abudefduf vaigiensis* (Quoy & Gaimard, 1825).

Dascyllus aruanus (Linnaeus, 1758)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "93. [CHÆTODON] p) *Abu dafur*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 65): "93. CHÆTODON [a] ABU DAFUR Arab. est charactere *Aruani* LINN. albus, fasciis tribus nigris: spinis Dors. 12. A. 2. *Djiddæ* habitat, rarior, inter corallia. spith. longit.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Chætodon*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *abu dafur*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu dafur.

Remarks: FORSSKÅL used the Arabic name 'abu dafur' as a substitute for a scientific name possibly to be designated for this *Chætodon* sp., which he possibly considered to be identical with *Chaetodon aruanus* Linnaeus, 1758. FABRICIUS in NIEBUHR (1775a) named *Chætodon abu dafur* in the text, but also stated that '*Abu dafur*' is the Arabic name. As the species name consists of two words, it is not considered binominal (ICZN, Art. 5), not meant as a species name (indication that it is the Arabic name), and therefore not considered as available as *Chaetodon abu dafur* Fabricius [ex Forsskål] in Niebuhr, 1775. Judging from the colour description and habitat, the species is identical with *Dascyllus aruanus* (Linnaeus, 1758), as already stated by RÜPPELL (1829: 39, *Pomacentrus aruanus*) and GÜNTHER (1862: 12), erroneously listed as *Chaetodon abudafar* by ESCHMEYER (2007).

L a b r i d a e – Wrasses

Cheilinus abudjubbe Rüppell [ex Forsskål], 1835

FORSSKÅL in NIEBUHR (1775a: XI): "34. [LABRUS i) LUNULATUS] β) lineis radiantibus circa oculos.".

FORSSKÅL in NIEBUHR (1775a: 37): "34. [LABRUS LUNULATUS] b) *Varietas* sine lunula fulva: lineis circa oculos radiantibus, rubris, longis.".

FORSSKÅL in NIEBUHR (1775a: 44): "B) *Dentibus* [*Scarus*] *Abu djubbe*: maxillis continuis, dentatis: denticulis subulatis, remotis.".

Locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Material: ZMUC P.5847 (holotype of *Cheilinus abudjubbe* Rüppell [ex Forsskål], 1835; paralectotype of *Labrus lunulatus* Forsskål in Niebuhr, 1775).

Genus name: *Labrus*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *lunulatus* (var. b).

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu djubbe, Sænuat abu djubbe.

Remarks: This variety was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Labrus lunulatus* var. β or var. b; neither of the two gives a variety name. The species was named (*Scarus*) *abu djubbe* in the teeth description on p. 44; however, the species name is not binominal as consisting of two words, and therefore not available as *Scarus abu djubbe* Fabricius [ex Forsskål], 1775. FORSSKÅL's description is the basis for RÜPPELL's (1835: 18) description of *Cheilinus abudjubbe* Rüppell [ex Forsskål], 1835, which is a valid species. The common name 'abu djubbe' is obviously attributed to this variety, though FABRICIUS in NIEBUHR (1775a) apparently confused the two varieties and listed 'abu djubbe' in the index for *Labrus lunulatus*, but in the text for *Labrus lunulatus* var. b. It is here assumed that the text version is correct.

Cheilinus lunulatus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "34. [LABRUS] i) LUNULATUS; squamis fasciatis. *Abu djubbe* vel *Dîk*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 37): "34. LABRUS LUNULATUS; *fusco-virescens, fasciis obscurioribus, squamis singulis fascia ferruginea, capite pectoreque rubro-guttato, lunula operculi pone fulva*.".

Type locality: – (Red Sea).

Type material: Lectotype: ZMUC P.4856 (dry skin) (listed as holotype by ESCHMEYER 2007), designated by KLAUSEWITZ & NIELSEN 1965: 17; see also pl. 7), see also MØLLER (2006).

Genus name: *Labrus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *lunulatus*.

Arabic names (Latinised, FABRICIUS in NIEBUHR): Abu djubbe?, Dik.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Labrus lunulatus*; the name is binominal in both the index and text, is accompanied by a diagnosis and description, and is therefore available as *Labrus lunulatus* Forsskål in Niebuhr, 1775. The species was considered as valid since WALBAUM (1792: 242–243, 246; double entry). FABRICIUS in NIEBUHR (1775a) confused the two varieties when assigning the common name (see above, remarks under *Cheilinus abudjubbe*).

Cheilio inermis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XI): "27. [LABRUS] b) INERMIS; nigro-guttatus. *Gbassek*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 34): "27. LABRUS INERMIS; *radiis pinnarum spinosis nullis; corpore lineari, oblongo, virente; vitta laterali nigro-guttata*.".

Type locality: "*Mochhæ*" (Al-Mukhā/Yemen).

Type material: Lectotype: ZMUC P.5739, as designated by KLAUSEWITZ & NIELSEN (1965: 16; see also pl. 6); paralectotype: ZMUC P.5740 (dry skin) (MØLLER 2006).

Genus name: *Labrus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *inermis*.

Arabic name (Latinised, FORSSKÅL): Ghassek; (FABRICIUS in NIEBUHR): Gbassek.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Labrus inermis*; the name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it is therefore available as *Labrus inermis* Forsskål in Niebuhr, 1775. The species was considered as valid since WALBAUM (1792: 262). It was subsequently re-named *Cheilio forskalii* Valenciennes in Cuvier & Valenciennes, 1839 (VALENCIENNES in CUVIER & VALENCIENNES 1839: 349), which is a junior synonym. This is one of the last fish species discovered by P. S. FORSSKÅL in May, June or July 1763. *Labrus hassek* Lacepède [ex Forsskål], 1801 (LACEPÈDE 1801: 444, 513, 515–516) is an unneeded new name for *Labrus inermis* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Coris julis (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XI): "21. SPARUS a) NILOTICUS; recte *Labrus julis*.".

Forsskål in Niebuhr (1775a: 31): "21. SPARUS niloticus ab *Hasselquist* descriptus (it. Palæst. p. 341) est *Labrus Julis, Linn.* ut character indicat; & nomen Gallicum *Girelle* (Labro Juli proprium). …".
Type locality: – (Marseille/France; not known from the Nile).
Remarks: *Sparus niloticus* Forsskål [ex Hasselquist] in Niebuhr, 1775 was not mentioned by Eschmeyer (2007); the name was only described in the Hasselquist (1762: 387) version [listed by Eschmeyer 2007 as not available, as published in a rejected work, see Anonymus (1914, 1956), Melville & Smith (1987: 330)]. Forsskål's version was published in synonymy of *Labrus julis* and is therefore not available. The species was not identified in the sense of Hasselquist, as Hasselquist's fish was a freshwater species from the Nile. The name was made available under the two names *Labrus niloticus* Walbaum [ex Forsskål & Hasselquist], 1792 (Walbaum 1792: 258–259) and *Sparus niloticus* Walbaum [ex Forsskål & Hasselquist], 1792 (Walbaum 1792: 300); they are junior synonyms of *Coris julis* (Linnaeus, 1758).

Coris julis (Linnaeus 1758)

Fabricius [ex Forsskål] in Niebuhr (1775a: XI): "26. LABRUS a) perdica; vittis dentatis. Πέρδικα.".
Fabricius [ex Forsskål] in Niebuhr (1775a: 34, part): "26. LABRUS perdica; *cauda æquali; vertice glabro; dorso recto; vittis utrinque dentatis, albido-flavicantibus.*".
Type locality: – (Turkey).
Genus name: *Labrus.*
Species name (Forsskål): –; (Fabricius in Niebuhr): *perdica.*
Remarks: In his draft, Forsskål used the Greek name Πέρδικα as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr (1775a) described the new species as *Labrus perdica*; the new name is binominal both in the index and in the text, is accompanied by a diagnosis and description, and would be available (based on the description) as *Labrus perdica* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The species was considered as valid by Walbaum (1792: 248). This is a composite species, based in part on *Coris julis* (Linnaeus 1758), and on *Labrus bergylta* Ascanius, 1767 (see below).

Coris julis (Linnaeus, 1758)

Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "[Labrus] *julis.*".
Locality: "Melita" (La Valletta/Malta).

Labrus bergylta Ascanius, 1767

Forsskål in Niebuhr (1775a: 34, part): "26. LABRUS perdica; *cauda aequali; vertice glabro; dorso recto; vittis utrinque dentatis, albido-flavicentibus.*".
Type locality: – (Turkey).
Genus name: *Labrus.*
Species name (Forsskål): –; (Fabricius in Niebuhr): *perdica.*
Remarks: The Turkish record of this new species is based in part on *Labrus bergylta* Ascanius, 1767, judging on the Turkish name 'Keklik balùk' (modern Turkish name 'Kikla', according to Fricke et al. 2007: 93). The species regularly occurs in the Marmara Sea near İstanbul, and was probably collected by Forsskål using the fishing vessel he chartered. This is a composite species, based in part on *Coris julis* (Linnaeus, 1758) (see above).

Labrus viridis (Linnaeus, 1758)

Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "Labrus *turdus* vulg.".
Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "[Labrus] *turdus virid. minor.*".
Locality: "Melita" (La Valletta/Malta).
Remarks: Two varieties of the species *Labrus turdus* Linnaeus, 1758 were recorded from Malta by Forsskål [ex Anonymus] in Niebuhr (1775a), the ordinary variety of *Labrus turdus*, and a variety named *Labrus turdus virid(is) minor.* The latter, if considered as a variety name, would not be binominal, and as neither was accompanied by a diagnosis, it would not be available. Both names are synonyms of *Labrus viridis* Linnaeus, 1758, which is considered as a valid species.

Pteragogus flagellifer (Valenciennes in Cuvier & Valenciennes, 1839)

Forsskål in Niebuhr (1775a: XI): "28. [LABRUS] c) ramentosus; ramentis longis.".
Forsskål in Niebuhr (1775a: 34–35): "28. LABRUS ramentosus; *fusco-virescens; ramentis spinarum dorsalium primarum, radio duplo longioribus.*".
Type locality: "Mochhæ" (Al-Mukhā/Yemen).
Genus name: *Labrus.*
Species name (Forsskål, Fabricius in Niebuhr): *ramentosus.*
Remarks: This species was described by both Forsskål and Fabricius in Niebuhr as *Labrus ramentosus*; it is binominal in both the index and text, and accompanied by a diagnosis and description; it is therefore available as *Labrus ramentosus* Forsskål in Niebuhr, 1775, and was treated as such by Bonnaterre (1788: 108), Gmelin (1789: 1293), and Bloch & Schneider (1801: 258). Unfortunately, this is a rarely used senior synonym of *Pteragogus flagellifer* (Valenciennes in Cuvier & Valenciennes, 1839). In order to preserve stability of nomenclature (preamble and Art. 23.2 of ICZN), an application to the International Commission on Zoological Nomenclature is needed to suppress the name *Labrus ramentosus.* The name was subsequently misspelled *Lutjanus ramentaceus* by Lacepède (1802: 183, 218), which is not an independent species description, but a spelling error explicitly based on *Labrus ramentosus.*

Symphodus ocellatus (Linnaeus, 1758)

Forsskål in Niebuhr (1775a: XI): "33. [LABRUS] h) ocellatus; ocello coccineo.".
Forsskål in Niebuhr (1775a: 37): "33. LABRUS ocellatus; *virescens; ocello coccineo pone utrumque oculum.*".
Type locality: "*Smirnae*" (İzmir/Turkey).
Genus name: *Labrus.*
Species name (Forsskål): *ocellatus (ocellaris)*; (Fabricius in Niebuhr): *ocellatus.*
Remarks: This is not an independent new species description, but an incorrect subsequent spelling (ICZN, Art. 33.3) of *Labrus ocellaris* Linnaeus, 1758; the emendation was done either by both Forsskål and Fabricius, or just by Fabricius in Niebuhr. The argument that Forsskål or Fabricius were not aware of Linnaean names is not valid (see Introduction). The spelling with the prevailing usage (ICZN, Art. 33.2.3.1), however, is *Symphodus ocellatus.* The obligatory name is therefore *Symphodus ocellatus* (Linnaeus, 1758), with the authorship changed to Linnaeus (1758), and the Linnaean spelling changed to *ocellatus.* Forsskål's spelling was treated as valid as *Labrus ocellatus* Bonnaterre [ex Forsskål], 1788, and by subsequent authors like Walbaum (1792: 249–250) and Bloch & Schneider (1801: 259) who erroneously treated it as separate from *Labrus ocellaris.* Today, the

species is common in the Aegean Sea near İzmir (FRICKE et al. 2007: 94).

Symphodus rostratus (Bloch, 1791)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "30. [LABRUS] e) SCINA; abdomine recto. Σκίνα.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 36): "30. LABRUS SCINA; *cauda integra; corpore virescente, nebulis albis flavisque; fovea inter oculos impressa; & ante foveam sulco impresso.*".

Type locality: "CONSTANTINOPOLI" (İstanbul/Turkey).

Genus name: *Labrus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *scina*.

Remarks: In his draft, FORSSKÅL used 'scina' as a substitute for a species name possibly to be designated. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Labrus scina*; the name is binominal in both the index and text, accompanied by a diagnosis and description; it would therefore be available as *Labrus scina* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. According to the description, it is an unused senior synonym of *Labrus rostratus* Bloch, 1791, and needs to be suppressed by an application to the International Commission on Zoological Nomenclature, in accordance with the preamble and Art. 23.2 of ICZN; the species is considered as valid as *Symphodus rostratus* (Bloch, 1791). The species is regularly found in the Bosporus and the Marmara Sea near İstanbul (FRICKE et al. 2007: 95), and was probably collected by FORSSKÅL when he chartered a fishing vessel.

Symphodus tinca (Linnaeus, 1758)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XI): "31. [LABRUS] f) LAPINA; rubro-maculatus. Λαπίνα.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 36): "31. LABRUS LAPINA; *cauda integra; pinnis pectoralibus flavis; Ventralibus cæruleis; reliquis violaceis, maculis cæruleis.*".

Type locality: "CONSTANTINOPOLI" (İstanbul/Turkey).

Genus name: *Labrus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *lapina*.

Remarks: In his draft, FORSSKÅL used the Greek name Λαπίνα as a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR (1775a) described the new species as *Labrus lapina*; the new name is binominal both in the index and in the text, is accompanied by a diagnosis and description, and would be available as *Labrus lapina* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The species was treated as valid by BONNATERRE (1788: 111), GMELIN (1789: 1293), WALBAUM (1792: 253–254) and BLOCH & SCHNEIDER (1801: 260–261). *Labrus lapina* is a junior synonym of *Labrus tinca* Linnaeus, 1758, with the currently used name *Symphodus tinca* (Linnaeus, 1758).

Symphodus tinca (Linnaeus 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "25. [LABRUS] b) *tinea*. Arab. *Chåddæjr*. P. Pect. flavis; V. viridibus. P. A. C. & D. viridibus, maculis violaceis.".

Locality: – (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Remarks: This is a spelling error for the Linnaean species *Labrus tinca*.

Thalassoma pavo (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[LABRUS] *pavo*.".

Locality: "Melita" (La Valletta/Malta).

Thalassoma purpureum (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "12. [SCARUS] d) PURPUREUS; psittacus marinus. *Durras el báhr*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 27–28): "12. SCARUS PURPUREUS; *obscure-viridis; vittis utrinque tribus purpureis: ventre cæruleo; pinnis dorsi & ani linea purpurea: caudæ medio truncata.*".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *purpureus*.

Arabic name (Latinised, FORSSKÅL): Durrat el báhr; (FABRICIUS in NIEBUHR): Durras el bahr.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus purpureus*. The name is binominal, and accompanied by a diagnosis and description; it is therefore available, and a valid species, with the currently used name *Thalassoma purpureum* (Forsskål in Niebuhr, 1775).

Thalassoma rueppellii (Klunzinger, 1871)

FORSSKÅL in NIEBUHR (1775a: X): "11. [SCARUS] c) GALLUS; venenatus. *Dîk el báhr*.".

FORSSKÅL in NIEBUHR (1775a: 26–27): "11. SCARUS GALLUS: *obscure-viridis, capitis abdominisque lineis violaceis, pinna caudæ bifurca; medio flava. An Labrus lunaris Linn.?*".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen).

Type material: Holotype: ZMUC P.5738 (see KLAUSEWITZ & NIELSEN 1965: 14, pl. 2; MØLLER 2006).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *gallus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Dik el bahr.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus gallus*. The name is binominal, and accompanied by a diagnosis and description; it is therefore available as *Scarus gallus* Forsskål in Niebuhr, 1775. It was regarded as a valid species by BLOCH & SCHNEIDER (1801: 245–246), and thought to be a possible synonym of *Labrus lunaris* [currently used name *Thalassoma lunare* (Linnaeus, 1758)] by later authors, but is now the senior synonym of *Thalassoma rueppellii* (Klunzinger, 1871), threatening that frequently used name. The name *Scarus gallus* is here rejected as unused in accordance with the preamble and Art. 23.2 of ICZN. To use the currently used name *Thalassoma rueppellii* (Klunzinger, 1871), an application to the International Commission on Zoological Nomenclature is advisable in order to place *Scarus gallus* on the index.

Xyrichtys novacula (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[CORYPHÆNA] *novacula*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il Janfru".

Xyrichtys novacula (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[BLENNIUS] *pentadactylus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is not an independent species description, but a misidentification of the species *Coryphaena pentadactylus* (non Linnaeus, 1758), erroneously or deliberately placed in the genus *Blennius*. *Coryphaena pentadactylus* would be

valid as *Iniistius pentadactylus* (Linnaeus, 1758); FORSSKÅL's [ex Anonymus] Maltese record, however, was based on *Xyrichtys novacula* (Linnaeus, 1758).

Scaridae – Parrotfishes

Chlorurus sordidus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "18. [SCARUS] k) SORDIDUS; fusco-ferrugineus. *Biss.*".

FORSSKÅL in NIEBUHR (1775a: 30): "18. SCARUS SORDIDUS, *maxillis rubentibus, corpore fusco ferrugineo, pinnis obscurioribus, cauda surgente pinna æquali.*".

FORSSKÅL locality: – (Red Sea).

Type locality: Off Hurghada, Egypt, Red Sea, 27°17'23"N, 33°48'52"E, 0–20 ft (as defined by neotype).

Type material: Neotype: USNM 202297, as selected by SCHULTZ (1969: 20).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *sordidus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Biss.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus sordidus*. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it is therefore available, and a valid species, as *Scarus sordidus* Forsskål in Niebuhr, 1775.

"*Hipposcarus harid* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "17. [SCARUS] i) HARID. Cauda basi squamosa. *Harîd.* [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 30): "17. SCARUS HARID: *cauda bifurca, media basi squamis septa.*".

FORSSKÅL in NIEBUHR (1775a: 44): "C) *Dentibus* [*Scarus*] *Harid*: maxillis crenatis, medio fissis.".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.5952 (see KLAUSEWITZ & NIELSEN 1965: 14, pl. 3; MØLLER 2006).

Genus name: *Scarus*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *harid*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Harîd.

Remarks: This species was described by FABRICIUS [ex FORSSKÅL] in NIEBUHR as *Scarus harid*; FORSSKÅL, however, did not include a scientific species name in his draft, but used the Arabic name 'harid' as a substitute for a Latin species name he possibly wanted to define; he left the note 'cauda basi squamosa' to select a scientific name later. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. The use of 'harid' as the species name was clearly decided and authored by FABRICIUS [ex FORSSKÅL]. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it would therefore be available as *Scarus harid* Fabricius [ex Forsskål] in Niebuhr, 1775, a valid species with the actual name *Hipposcarus harid* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN.

Scarus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: X): "SCARUS. SCARUS: novum genus Σκάρος. CHARACTER GENERICUS: *Dentium loco maxillæ ipsæ eminentes, margine dentato-crenatæ, osseæ.*".

FORSSKÅL in NIEBUHR (1775a: 25): "SCARUS novum genus antiquo nomine Σκάρος. Character genericus: Dentium loco maxillae ipsae eminentes, margine dentato-crenatae, osseae.".

Type species: *Scarus psittacus* Forsskål in Niebuhr, 1775 (subsequently designated by JORDAN & GILBERT 1883: 93).

Remarks: This is marked to be a new genus description, and accompanied by a diagnosis. The diagnosis, however, is not characteristic for one of the modern genera in Scaridae, but only for the family Scaridae itself. Unfortunately, the species listed under the generic name indicate that the genus was also of a composite origin, including species now classified in various families. The first species described under the new genus name is *Scarus siganus; rivulatus*, named in the index on p. X *Scarus rivulatus* (new genus: *Siganus*), i.e. *Siganus rivulatus* (see below). The next following species would be *Scarus stellatus*, which is again a siganid fish (*Siganus stellatus*, see below). The third and fourth species are *Scarus gallus* and *S. purpureus* which are based on species of *Thalassoma*, i.e. labrid fishes. The fifth species, *Scarus ghobban*, is the first to be a scarid fish in actual classification. However, *Scarus psittacus* was subsequently designated as the type species by JORDAN & GILBERT (1883: 93). FORSSKÅL in NIEBUHR's (1775) new name and diagnosis, however, refers to the ancient Greek fish Σκάρος, which is *Sparisoma cretense*. Therefore, *Sparisoma cretense* would be the originally intended type species, i.e. the '*Labrus scarus* cretic.' listed on p. XIX. Therefore, *Scarus* Forsskål in Niebuhr, 1775 would be the senior synonym of *Sparisoma* Swainson, 1839 (SWAINSON 1839: 172, 227). An opinion of the International Commission on Zoological Nomenclature will be necessary to stabilise the present usage of the name.

Scarus ferrugineus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: X): "15. [SCARUS] g) FERRUGINEUS; ore viridi. *Abu meles.*".

FORSSKÅL in NIEBUHR (1775a: 29): "15. SCARUS FERRUGINEUS; *corpore fusco-ferrugineo: maxillis margineque pinnarum exteriori viridibus: cauda æquali.*".

FORSSKÅL locality: – (Red Sea).

Type locality: Dahab, northwest coast of Gulf of Aqaba, Red Sea, 12 m (as defined by neotype).

Type material: Neotype: BPBM 18158, as selected by RANDALL & ORMOND (1978: 245).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *ferugineus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu meles.

Remarks: This species was described by both FORSSKÅL and FABRICIUS as *Scarus ferrugineus*. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it is therefore available, and a valid species, as *Scarus ferrugineus* Forsskål in Niebuhr, 1775.

"*Scarus ghobban* Forsskål in Niebuhr, 1775"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "13. [SCARUS] e) GHOBBAN; lituratus. *Ghobban.*".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 28): "13. SCARUS GHOBBAN; *cauda æquali, maxillis albidis; lituris capitis & pinnarum margine exteriori viridi-cæruleis.*".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Scarus*.

Species name (Forsskål): – (*lituratus*); (FABRICIUS in NIEBUHR): *ghobban*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Ghobban.

Remarks: This species was described by FABRICIUS [ex FORSSKÅL] in NIEBUHR as *Scarus ghobban*; in his draft, however, FORSSKÅL did not include a scientific species name, but used the Arabic name 'ghobban' as a substitute for a Latin species

name possibly to define, and possibly planned to use '*lituratus*' as mentioned in the index, where '*lituratus*' stands in the position where usually FORSSKÅL's species names are found. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. The use of 'ghobban' as the species name was clearly decided and authored by FABRICIUS [ex FORSSKÅL]. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it would therefore be available as *Scarus ghobban* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The species was treated as valid by BONNATERRE (1788: 95) and later authors. The species name was subsequently misspelled as *ghoban* by WALBAUM (1792: 687, *Scarus ghoban*) and KLUNZINGER (1871: 563–564, *Pseudoscarus ghoban*).

Scarus niger Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: X): "14. [SCARUS] f) NIGER. *Chadri.*".

FORSSKÅL in NIEBUHR (1775a: 28–29): "14. SCARUS NIGER: *ovato-oblongus, nigro-fuscus: labiis rubris: maxillis lituris capitis pinnarumque, exceptis pectoralibus; margine exteriori viridi-cœruleis.*".

Type locality: – (Red Sea).

Type material: Holotype: ZMUC P.5951 (see KLAUSEWITZ & NIELSEN 1965: 14, pl. 3; MØLLER 2006).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *niger*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Chagri.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus niger*. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it is therefore available, and a valid species, as *Scarus niger* Forsskål in Niebuhr, 1775. *Scarus chadri* Lacepède [ex Forsskål], 1802 (LACEPÈDE 1802: 2, 12) is an unneeded new name for *Scarus niger* Forsskål in Niebuhr, 1775; it is available, but a junior synonym.

Scarus psittacus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: X): "16. [SCARUS] h) PSITTACUS; viridi-flavus. *Durras el barr.* [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 29): "16. SCARUS PSITTACUS: *virescens, lineis flavicantibus, pinnarum margine, vitta abdominali, characteribus capitis cœruleis.*".

FORSSKÅL locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type locality: Sharm-el-Sheijkh, Sinai, Egypt, Red Sea (as defined by neotype).

Type material: Neotype: USNM 201805, as selected by SCHULTZ (1969: 7); RANDALL & ORMOND (1978) disagreed and selected a new BPBM neotype, which is not valid, unless the International Commission on Zoological Nomenclature suppresses the old neotype.

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *psittacus*.

Arabic name (Latinised, FORSSKÅL): Durrát el barr; (FABRICIUS in NIEBUHR): Durras el barr.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus psittacus*. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it is therefore available, and a valid species, as *Scarus psittacus* Forsskål in Niebuhr, 1775. This species was re-named *Pseudoscarus forskalii* Klunzinger [ex Forsskål], 1871 (KLUNZINGER 1871: 566–567).

Sparisoma cretense (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[LABRUS] *scarus cretic.*".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[LABRUS] *scarus varius.*" Local Maltese name: "Il Bricchese".

Locality: "Melita" (La Valletta/Malta).

Remarks: It is unclear if '*cretic.*' and '*varius*' are meant as two subspecies or varieties of the species *Labrus scarus* Linnaeus, 1758, or not. If so, they would be names only (nomina nuda), as *Labrus scarus creticus* Forsskål [ex Anonymus] in Niebuhr, 1775 and *Labrus scarus varius* Forsskål [ex Anonymus] in Niebuhr, 1775; none of them would be available as neither was accompanied by a diagnosis nor an indication. Both would be synonyms of the species *Sparisoma cretense* (Linnaeus, 1758).

Ammodytidae – Sand lances

Gymnammodytes cicerelus (Rafinesque-Schmaltz, 1810)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "AMMODYTES *tobianus.*".

Locality: "Melita" (La Valletta/Malta).

Remarks: This record of the species *Ammodytes tobianus* (non Linnaeus, 1758) is obviously based on the only Mediterranean species of ammodytid fish, *Gymnammodytes cicerelus*.

Trachinidae – Weeverfishes

Trachinus sp.

FORSSKÅL in NIEBUHR (1775a: XIV): "4. TRACHINUS. Δρακάινα. Acutissime pungit.".

Localities: – (İstanbul/Turkey and/or İzmir/Turkey).

Remarks: Here, only the genus name is given without diagnosis. The only information is that the fish is stinging severely, but this is true for any species of the genus. The record cannot be assigned to species level. In the area, four species of trachinids are found (FRICKE et al. 2007: 95–96): *Echiichthys vipera* (Cuvier, 1829); *Trachinus araneus* Cuvier [ex Risso] in Cuvier & Valenciennes, 1829; *Trachinus draco* Linnaeus, 1758; *Trachinus radiatus* Cuvier, 1829.

Trachinus sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "TRACHINUS *draco.*".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Majuro ta rocca".

Remarks: Again, this record is based on a name only, and cannot be assigned to species level; it could have been based on either Mediterranean species of trachinid fish (see above).

Uranoscopidae – Stargazers

Uranoscopus scaber Linnaeus 1758

FORSSKÅL in NIEBUHR (1775a: XIV): "3. URANOSCOPUS *scaber.* Turc. *Kurba.* Constantinop. Βάζραχος. Smirnae *Βέφος* vel *Λύχνος*.".

Localities: "Constantinop." (İstanbul/Turkey); "Smirna" (İzmir/Turkey).

Remarks: This is undoubtedly the Linnaean species *Uranoscopus scaber*. The modern Turkish name is 'Kurbağa balığı' (FRICKE et al. 2007: 96).

B l e n n i i d a e – Combtooth blennies

Coryphoblennius galerita (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[BLENNIUS] *galerita*.".

Locality: "Melita" (La Valletta/Malta).

Coryphoblennius galerita (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[BLENNIUS] *galea*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a name only, listed as *Blennius galea* Forsskål in Niebuhr, 1775. This is not an independent species description, but a spelling error for *Blennius galerita* Linnaeus, 1758, and thus a double entry of that species.

Salaria Bath [ex Forsskål], 1977

FORSSKÅL in NIEBUHR (1775a: X): "3. GADUS vel novum genus SALARIA. Σαλάρια.".

FORSSKÅL in NIEBUHR (1775a: XIV, part): "(5). *Gadum* Σαλαρία, solent Græci infantibus offere pro medicamine masticatorio, dum saliva nimis definit." (In wrong line after diagnosis of *Gadus mediterraneus*).

FORSSKÅL in NIEBUHR (1775a: 22–23): "3. GADUS an BLENNIUS? An potius novus, nomine SALARIÆ: dorso monopterygio, cirrhis nullis.".

Localities: "ALEXANDRIA & in *Archipelago*." (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea; islands in the Aegean Sea/Greece).

Remarks: FORSSKÅL was uncertain according to his notes whether this was a *Gadus* sp. or a new genus, *Salaria*, defining it as having a single dorsal fin and without barbels, and adding a short description. *Gadus salaria* Walbaum [ex Forsskål], 1792 (WALBAUM 1792: 143) (here, '*salaria*' is taken as a species name) is based on FORSSKÅL's description and would be the first available species name assignment, therefore providing a potential type species for FORSSKÅL's genus. *Gadus salaria* is a senior, but unused, synonym of *Salaria basilisca* (Valenciennes in Cuvier & Valenciennes, 1836), according to BATH (1977: 208); JORDAN & EVERMANN (1898: 2377) already quoted *Blennius basiliscus* as the type species. For availability according to Art. 11.5 of ICZN, a name must be used as valid for a taxon when proposed, unless it was first published as a junior synonym and subsequently made available under the provisions of Art. 11.6.1. In this case, the name is not clearly defined as a valid name, as both FORSSKÅL and FABRICIUS in NIEBUHR were uncertain whether this was a *Gadus* or a new genus *Salaria*. The name *Salaria* Forsskål in Niebuhr, 1775 is therefore not available as a generic name. GÜNTHER (1861: 220) was the first to list FORSSKÅL's species on pp. XIV and 22 as '?' in the synonymy of *Blennius basiliscus*, but without mentioning the genus name *Salaria* which he apparently did not consider as valid. JORDAN & EVERMANN (1898: 2377) were the first to take *Salaria* as generic name, in the synonymy of *Blennius*, and referred to *Blennius basiliscus* as the type species without further comments, probably on the basis of GÜNTHER (1861); they were therefore the first to assign a species name to the genus *Salaria*. As this name was assigned in synonymy, the name is not considered valid either. According to Art. 11.6.1 of ICZN, a name published in synonymy is only available if used as a valid name before 1961. This is not the case for *Salaria*, so neither the quotation by JORDAN & EVERMANN (1917: 33) nor by any other of the subsequent authors mentioning the generic name in the synonymy of *Blennius* can be considered as valid. The first available version of the generic name *Salaria* is that of BATH (1977: 208); BATH [ex FORSSKÅL] is therefore the author of the genus, with the name *Salaria* Bath [ex Forsskål], 1977; BATH gives *Blennius salaria* (erroneously with an authorship of 'Valenciennes in Cuvier & Valenciennes, 1836') as the type species, which is a junior synonym of *Blennius basiliscus*. Therefore, *Gadus salaria* Walbaum [ex Forsskål], 1792 is the type species of *Salaria*. – However, this complicates the matter, as *Salaria* Bath [ex Forsskål], 1977 is a junior synonym of *Ichthyocoris* Bonaparte, 1840. The valid name for the genus would therefore be *Ichthyocoris*. In accordance with Art. 23.2 of ICZN, the unused generic name *Ichthyocoris* Bonaparte, 1840 would threaten nomenclatural stability and is here rejected; a petition to the International Commission on Zoological Nomenclature to suppress the name *Ichthyocoris* will be needed to continue the usage of the name *Salaria* as the valid name for the genus.

?Salaria pavo (Risso, 1810)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "BLENNIUS *alauda*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a name only (nomen nudum), which is neither accompanied by a diagnosis nor an indication, and therefore not available as *Blennius alauda* Forsskål [ex Anonymus] in Niebuhr, 1775. Judging from the Italian name 'alauda', this record may have been based on *Salaria pavo* (Risso, 1810).

Salarias fasciatus (Bloch, 1786)

FORSSKÅL in NIEBUHR (1775a: X): "4. BLENNIUS GATTORUGINE; torvus. *Koschar ed djin*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 23): "4. BLENNIUS GATTORUGINE: *dorsi pinna unica cum pinna caudæ connata; capite obtusissimo, cirrhis tribus supra utrumque oculum, et utrinque senis in postico vertice*.".

Locality: – (Red Sea).

Material: ZMUC P. 75421 (1) (syntype of *Salarias quadripennis* Cuvier, 1816) (see KLAUSEWITZ & NIELSEN 1965: 13; MØLLER 2006).

Remarks: This is not an independent new species description, as assumed by KLAUSEWITZ & NIELSEN (1965: 13), but a misidentification of *Blennius gattorugine* (non Linnaeus, 1758). A specimen is still extant, and was identified as *Salarias fasciatus* (Bloch, 1786) by KLAUSEWITZ & NIELSEN (1965: 13). *Salarias quadripennis* Cuvier [ex Forsskål], 1816 (CUVIER 1816: 251) was described on the basis of FORSSKÅL's *Blennius gattorugine* (non Linnaeus, 1758); it is a junior synonym of *Blennius fasciatus* Bloch, 1786, which is valid with the currently used name *Salarias fasciatus* (Bloch, 1786). The *Salarias quadripennis* of RÜPPELL (1830: 112–113) is not an independent species description as indicated by ESCHMEYER (2007), but was explicitly based on the *Salarias quadripennis* of CUVIER.

C a l l i o n y m i d a e – Dragonets

?Callionymus pusillus Delaroche, 1809

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[COTTUS] *dracunculus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is not an independent species description, but the record is based on *Callionymus dracunculus* Linnaeus, 1758; it was placed either deliberately or erroneously in the genus *Cottus*. The name *Callionymus dracunculus* was suppressed for the purpose of priority but not homonymy, and the name was placed on the Official Index (Opinion 1658: Anonymus 1991). The record was most probably based on *Callionymus*

pusillus Delaroche, 1809, the only callionymid fish species that may be frequently found on shallow sand bottoms in Malta.

Gobiidae – Gobies

Gobiidae, indet.

FORSSKÅL in NIEBUHR (1775a: XIV): "9. [GOBIUS] b) *aphya*. Κοβίδια. Turc. *Kaja baluk*. Arab. *Bukrusch*. ...".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GOBIUS] *aphya*.".

Localities: "Constantinopoli" (İstanbul/Turkey); probably also Alexandria (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea); "Melita" (La Valletta/Malta).

Remarks: This is the species *Gobius aphya* Linnaeus, 1758, which was originally described from River Nile/Egypt. The species account on p. 9 is accompanied by a short diagnosis, but cannot be assigned to a species within the family Gobiidae. The Turkish name 'Kayabalığı' refers to various species of larger gobies (FRICKE et al. 2007).

Gobiidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[SCORPÆNA] *scorpius*.".

Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il Mazzun".

Remarks: This is not an independent species description, but again based on *Cottus scorpius* (non Linnaeus, 1758). This is an erroneous double entry of one species under two different genus names, and accompanied by two different local names (see above). According to the Maltese name, this was a misidentification as the actual vernacular Maltese name 'Mazzun' (Anonymus 2007b) refers to various species of Gobiidae.

Cryptocentrus arabicus (Gmelin [ex Forsskål], 1789)

FORSSKÅL in NIEBUHR (1775a: X): "5. GOBIUS. a) ANGUILLARIS; minimus.".

FORSSKÅL in NIEBUHR (1775a: 23–24): "5. GOBIUS. ANGUILLARIS: *cute mollissima, squamis adnatis: pinnis dorsi primis, radiis 5; posterioribus eminentibus, filiformibus*.".

Locality: "Djiddæ" (Jeddah, Juddah/Saudi Arabia).

Remarks: This is a misidentification of the species *Gobius anguillaris* (non Linnaeus, 1758), not an independent species description. The species was subsequently described as *Gobius arabicus* Gmelin [ex Forsskål], 1789 (GMELIN 1789: 1198), a species currently accepted as valid which is now named *Cryptocentrus arabicus* (Gmelin [ex Forsskål], 1789). This species, however, was previously available as *Gobius djiddensis* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 64). As the latter is an unused name, it is here rejected; a petition to the International Commission on Zoological Nomenclature will be needed to suppress it and conserve *Gobius arabicus* Gmelin [ex Forsskål], 1789.

Gobius niger Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "GOBIUS *niger*.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GOBIUS] *jozo*.".

Locality: "Melita" (La Valletta/Malta).

Gobius paganellus Linnaeus 1758

FORSSKÅL in NIEBUHR (1775a: XIV): "8. GOBIUS a) *paganellus*. Γοβιός.".

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[GOBIUS] *paganellus*.".

Localities: – (Turkey); "Melita" (La Valletta/Malta).

Remarks: The Turkish record is based on the Linnaean species *Gobius paganellus*, which is regularly found in shallow water, both around İstanbul and İzmir. The Maltese record is a name only, and the identification cannot be verified.

Yongeichthys nebulosus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "6. [GOBIUS] b) NEBULOSUS, pinnæ d. radio prolongato. *Hout ed djinn*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 24): "6. GOBIUS NEBULOSUS: *squamis asperis, fusco-nebulosis: pinnæ dorsalis primæ radio secundo filo longo nigro*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Gobius*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *nebulosus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Hout ed djinn.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Gobius nebulosus*; the description was accompanied by a diagnosis and description; the name is available as *Gobius nebulosus* Forsskål in Niebuhr, 1775. It was treated as valid since BONNATERRE (1788: 64–65) and WALBAUM (1792: 199–200).

Ephippidae – Spadefishes

Platax orbicularis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XII): "79. CHÆTODON a) ORBICULARIS; dorso ascendente. *Kanaf*.".

FORSSKÅL in NIEBUHR (1775a: 59): "79. CHÆTODON ORBICULARIS; *cinereo-fuscus; subrotundus; spinis dorsalibus nullis*. Arab. major *Kanaf*: parvus *Dakar*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Holotype: ZMUC P.5168 (dry skin) (see KLAUSEWITZ & NIELSEN 1965: 23, pl. 30; MØLLER 2006).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *orbicularis*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Kanaf (larger), Dakar (small).

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon orbicularis*; the name is binominal in both text and index, is accompanied by a diagnosis and description, and therefore available as *Chaetodon orbicularis* Forsskål in Niebuhr, 1775. The species is valid, with the currently used name *Platax orbicularis* (Forsskål in Niebuhr, 1775).

"*Platax teira* (Forsskål in Niebuhr, 1775)"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "82. [CHÆTODON] d) TEIRA; pinna dors. corpore duplo longiore. *Teyra*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 60–61): "82. CHÆTODON TEIRA; *corpore rhombeo, fuscescente; fascia transversa duplici obscuriori: pinnis ventralibus, ani & caudæ falcatis, corpore longioribus*.".

FORSSKÅL [ex BAURENFEIND] in NIEBUHR (1776: 7): "CHÆTODON Teira. Pag. 60, n. 82. (TAB. XXII)".

Type locality: "LOHAJÆ" (Al-Luhayya/Yemen).

Genus name: *Chætodon*.

Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *teira*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Dáakar (large), Teyra (small).

Remarks: In his draft, FORSSKÅL used the Arabic name 'teira' as

a substitute for a Latin name possibly to be selected. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS in NIEBUHR described the species as *Chætodon teira*; the name is binominal in both text and index, is accompanied by a diagnosis and description, and therefore would be available as *Chaetodon teira* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 417–418). FORSSKÅL [ex BAURENFEIND] in NIEBUHR (1776: pl. 22) illustrated a young specimen of this species. *Chetodon daakar* Bonnaterre [ex Forsskål], 1788 (BONNATERRE 1788: 81, pl. 95, fig. 389) was described as an unneeded replacement name of "*Chaetodon teira* Forsskål in Niebuhr, 1775"; it is a junior synonym.

S i g a n i d a e – Rabbitfishes

"*Siganus* Forsskål in Niebuhr, 1775"

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: X): "nov. genus SIGANUS" (named under listing of *Scarus rivulatus*).

Type species: *Siganus rivulatus* Forsskål & Niebuhr in Niebuhr, 1775.

Remarks: The species named by FORSSKAL in his draft *Scarus siganus* was renamed by FABRICIUS in NIEBUHR as a new genus, *Siganus*, attributed to the first species listed under the new genus name *Scarus*. The new genus was not accompanied by a diagnosis, and is only available by the type species designation by FABRICIUS in NIEBUHR. Though the name *Siganus* was published in synonymy of *Scarus*, it would be considered to be available as *Siganus* Fabricius [ex Forsskål] in Niebuhr, 1775, according to ICZN, Art. 15.1 and 11.9.3.4, the authorship pending a decision of ICZN.

"*Siganus rivulatus* Forsskål in Niebuhr, 1775"

FORSSKÅL & NIEBUHR in NIEBUHR (1775a: X): "9. [SCARUS] a) RIVULATUS: *Djezavi* vel *Sigıân*. [..., Arabic name] nov. genus: SIGANUS.".

FABRICIUS [ex FORSSKÅL & NIEBUHR] in NIEBUHR (1775a: 25–26): "9. SCARUS SIGANUS; RIVULATUS; *maxillis continuis, complanatis, margine serrato-denticulatis: denticulis approximatis, filiformibus; a medio labio paulatim decrescentibus*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 44): "A) *Sc.* [*Scarus*] *dentibus Sidjan*; maxillis continuis: denticulis approximatis, filiformibus.".

Type localities: "*Lohajæ*" (Al-Luhayya/Yemen); "*Basræ*" (Al-Basrah/Iraq, 30°30'N 47°47'E).

Type material: Lectotype: ZMUC P.6689 (dry skin) (either from Al-Luhayyah, collected by FORSSKÅL but returned by NIEBUHR, or collected by NIEBUHR at Al-Basrah), as designated by KLAUSEWITZ & NIELSEN (1965: 13–14, pl. 2); paralectotype: ZMUC P.6690 (dry skin) (MØLLER 2006).

Genus name: *Siganus* (or *Scarus*?).

Species name (FORSSKÅL): *siganus*; (FABRICIUS in NIEBUHR): *rivulatus*.

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Djezavi, Sidjan, Sigian.

Remarks: This species was obviously intended to be named *Scarus rivulatus* by FORSSKÅL in his draft, as a member of the genus *Siganus*. It was FABRICIUS in NIEBUHR who apparently thought that this may represent another new genus, and added the name *Siganus* new genus, which was named for the Arabic name Sidjan or Sigian. It is not clear whether the remark on p. 26 was added by FABRICIUS in NIEBUHR or FORSSKÅL, neither whether the specimen ZMUC P.6689 was collected by NIEBUHR or FORSSKÅL, though it was evidently sent to Copenhagen by NIEBUHR, not FORSSKÅL. NIEBUHR at least added the remark on the Al-Basrah locality (FORSSKÅL never visited Al-Basrah/Iraq), which was accompanied by part of the description. It is therefore evident that the authorship of the name must be attributed (at least in part) to NIEBUHR. The name was used in two different versions, *Scarus rivulatus* (n. gen. *Siganus*) on p. X, and *Scarus siganus*; *rivulatus* on p. 25. The second version is accompanied by a diagnosis and description, while the first version is a mere listing. Though the second version is not binominal and therefore not available, giving two alternative names for the species (ICZN, Art. 5), both versions are considered to be linked together by the species code '9', and the name is available by indication (ICZN, Art. 12.2.2) through the first version, (*Scarus*) *Siganus rivulatus*. As the name was intended to belong to the new genus *Siganus*, though listed under *Scarus*, it would be be quoted without parentheses as *Siganus rivulatus* Forsskål & Niebuhr in Niebuhr, 1775, the authorship pending a decision of ICZN. This species was later named *Scarus siganus* Bonnaterre [ex Forsskål], 1788), and *Amphacanthus sigan* Klunzinger [ex Forsskål], 1871 (KLUNZINGER 1871: 502), which are junior synonyms. The *Amphacanthus siganus* of RÜPPELL (1829: 44, pl. 11, fig. 1) is not an independent species description, but based on the *Scarus siganus* of BONNATERRE (ex FORSSKÅL). – "*Scarus sidjan* Forsskål in Niebuhr, 1775" {would be *Scarus sidjan* Fabricius [ex Forsskål] in Niebuhr, 1775} is another name for this species, out of the version on p. 44 '*Scarus dentibus Sidjan*', meaning 'teeth of *Scarus sidjan*'; it is binominal, accompanied by a diagnosis, available, and an unused synonym of *Siganus rivulatus* Forsskål & Niebuhr in Niebuhr, 1775. I hereby act as the first reviser of this case to select *Scarus rivulatus* as the senior synonym. The *Scarus sidjan* of LACEPÈDE (1802: 1, 6) is not an independent species description, but based on "*Scarus sidjan* Forsskål in Niebuhr, 1775".

Siganus stellatus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: X): "10. [SCARUS] b) STELLATUS. *Ghæjtbán*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 26): "10. SCARUS STELLATUS; *ovalis*; *fasciis annulis cæruleo-pallidis, subhexagonis, undique contiguis*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Scarus*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *stellatus*.

Arabic name (Latinised, FORSSKÅL): Ghaejthan; (FABRICIUS in NIEBUHR): Ghajtbán.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Scarus stellatus*. It is identical in both versions, binominal, accompanied by a diagnosis and description, and thus available as *Scarus stellatus* Forsskål in Niebuhr, 1775, which was treated as valid since BONNATERRE (1788: 94) and WALBAUM (1792: 691). *Amphacanthus nuchalis* Valenciennes in Cuvier & Valenciennes [ex Forsskål], 1835 (VALENCIENES in CUVIER & VALENCIENNES 1835: 140) is an unneeded new name for *Scarus stellatus* Forsskål; it is available, and a junior synonym.

A c a n t h u r i d a e – Surgeonfishes

Acanthurus Forsskål in Niebuhr, 1775

FORSSKÅL in NIEBUHR (1775a: 59): "[CHÆTODON] c) ACANTHURUS: dentibus unius seriei, rigidis, acutis, contiguis, vel simplicibus vel lobatis. Cauda in utroque latere aculeo uno vel

pluribus; exserto & rigido; vel mobili & recondendo. Diversum prorsus a Chætodonte Genus; aliquando propriam constituens familiam.".

Type species: *Teuthis hepatus* Linné, 1766 (subsequent designation; see below).

Remarks: The name *Acanthurus* was used by both FORSSKÅL and FABRICIUS in NIEBUHR (1775a) as a new subgenus name, providing a diagnosis, and FORSSKÅL even stated that it is different enough from *Chaetodon* to be in future separated on the family level. The genus-group name is here considered as available as *Acanthurus* Forsskål in Niebuhr, 1775. The diagnosis includes characters of *Acanthurus* and *Naso*. The type species was subsequently designated by DESMAREST (1874: 246) as *Teuthis hepatus* Linné, 1766 [now *Paracanthurus hepatus* (Linné, 1766)]. This, however, causes problems, as *Acanthurus* Forsskål in Niebuhr, 1775 would be the senior synonym of *Paracanthurus* Bleeker, 1863. The next available genus-group name for *Acanthurus* of current usage would be *Harpurus* Forster, 1788 [FORSTER 1788: 84–85; type species: *Harpurus fasciatus* Forster in Bloch & Schneider, 1801 by monotypy, which is a synonym of *Acanthurus triostegus* (Linnaeus, 1758)]. A petition to the International Commission on Zoological Nomenclature will be needed to stabilise the current usage of the names *Acanthurus* and *Paracanthurus*.

Acanthurus gahhm (Gmelin [ex Forsskål], 1789)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "[90. CHÆTODON m) NIGRO-FUSCUS] β) *Gahhm*.".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 64): "90. [CHÆTODON NIGROFUSCUS] b) GAHHM Arab. ægre ab hoc distinguitur; nisi colore undique *nigro*: basi P. C. violacea: ...".

Type locality: – (Red Sea).

Genus name: *Chætodon*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *nigrofuscus* (var. b).

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Gahhm.

Remarks: This was intended as an unnamed variation of *Chætodon nigrofuscus* by both FORSSKÅL and FABRICIUS in NIEBUHR; the name 'Gahhm' in the index on p. XIII and in the text on p. 64 clearly indicated to be the Arabic name, not the scientific name. Therefore, the name (and spelling) *Chaetodon gahhm* is not available out of NIEBUHR's (1775a) publication. The first available usage with the spelling *Chaetodon gahm* is by GMELIN [ex FORSSKÅL], 1789 (GMELIN 1789: 1268–1269); the name is therefore available as *Chaetodon gahm* Gmelin [ex Forsskål], 1789. A previous author, BONNATERRE (1788: 83), just named the species 'Le Gahhm' without presenting a scientific name. It is a valid species, the spelling of the name, however, has to be changed to '*gahhm*' due to prevailing subsequent usage (ICZN, Art. 33.2.3.1), with the currently used name *Acanthurus gahhm* (Gmelin [ex Forsskål], 1789).

Acanthurus nigrofuscus (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XIII): "90. [CHÆTODON] m) NIGRO-FUSCUS. *Tæga*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 64): "90. CHÆTODON NIGROFUSCUS; *cauda utrinque spine recumbente*.".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Chætodon*.

Species name (FORSSKÅL): *nigro-fuscus*; (FABRICIUS in NIEBUHR): *nigrofuscus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Tæga.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon nigrofuscus* (version on p. 64; in the index as *Chætodon nigro-fuscus*), and was distinguished in the remarks from *Chaetodon nigricans* Linnaeus, 1758 as having an undivided caudal fin. It is binominal in both versions, accompanied by a diagnosis and description, and thus available as *Chaetodon nigrofuscus* Forsskål in Niebuhr, 1775. The species was treated as valid since WALBAUM (1792: 438).

Acanthurus sohal (Gmelin [ex Forsskål], 1789)

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XIII): "89. [CHÆTODON] l) SOHAL; fossula vulneriformi. *Sohal*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 63–64): "89. CHÆTODON SOHAL; *cauda utrinque carina ossea, in fossula rubra*.".

Type locality: – (Red Sea); – "Aliis" (Red Sea).

Type material: Lectotype: ZMUC P.6749 (dry skin); paralectotype: ZMUC P.6750 (dry skin) (MØLLER 2006). Lectotype designation by KLAUSEWITZ & NIELSEN (1965: 24; see also pl. 34).

Genus name: *Chætodon*.

Species name (FORSSKÅL): – (or *Chætodon lineatus* [Linnaeus, 1758]?); (FABRICIUS in NIEBUHR): *sohal* (or *Chætodon lineatus* [Linnaeus, 1758]?).

Arabic names (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Sohal, Sahal, Schausch.

Remarks: FORSSKÅL used the Arabic name 'sohal' as a substitute for a Latin name possibly to be designated, but was not sure if this species was a synonym of *Chaetodon lineatus* Linnaeus, 1758. FABRICIUS in NIEBUHR (1775a) described it as *Chaetodon sohal*, but again stated that this may be *Chaetodon lineatus*. Most understandably, FORSSKÅL had planned to solve the case later, but never did, nor did FABRICIUS in NIEBUHR (1775a). As neither FORSSKÅL nor FABRICIUS in NIEBUHR (1775a) clearly decided how to name the species, the name is not available. The first available usage of the name is *Chaetodon sohar* of Gmelin [ex Forsskål], 1789 (GMELIN 1789: 1268). The species was treated as valid since WALBAUM (1792: 441–442); the spelling of the name, however, has to be changed to '*sohal*' due to prevailing subsequent usage (ICZN, Art. 33.2.3.1). The species has the currently used name *Acanthurus sohal* (Gmelin [ex Forsskål], 1789). The species was subsequently described by BLOCH & SCHNEIDER (1801: 216) as *Acanthurus carinatus*, besides another species account on *Acanthurus sohal* (see BLOCH & SCHNEIDER 1801: 215); *Acanthurus carinatus* is a junior synonym of *Acanthurus sohal* (Gmelin [ex Forsskål], 1789).

Naso unicornis (Forsskål in Niebuhr, 1775)

FORSSKÅL in NIEBUHR (1775a: XIII): "88. [CHÆTODON] k) UNICORNIS; fronte cornuta. *Abu garn*. [..., Arabic name]".

FORSSKÅL in NIEBUHR (1775a: 63): "88. CHÆTODON UNICORNIS *fronte cornuta; cauda carinis utrinque duabus, elatis*.".

FORSSKÅL [ex BAURENFEIND] in NIEBUHR (1776: 7): "CHÆTODON unicornis. Pag. 63, n. 88. (TAB. XXIII)".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Type material: Lectotype designated by FRICKE (1999: 549) as the specimen illustrated by FORSSKÅL [ex BAURENFEIND] in NIEBUHR (1776: pl. 23).

Genus name: *Chætodon*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *unicornis*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu garn.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Chætodon unicornis*. It is binominal in both versions, accompanied by a diagnosis and descrip-

tion, and thus available as *Chaetodon unicornis* Forsskål in Niebuhr, 1775. The species was treated as valid since Bonnaterre (1788: 82) and Walbaum (1792: 440). It was illustrated by Forsskål [ex Baurenfeind] in Niebuhr (1776: pl. 23). *Monoceros biaculeatus* Bloch & Schneider [ex Forsskål], 1801 (Bloch & Schneider 1801: 180–181) was subsequently described as a new name for Forsskål's *Chaetodon unicornis*, and is a junior synonym. – *Naso fronticornis* Lacepède [ex Commerson, Forsskål], 1801 (Lacepède 1801: 105, 106–110, pl. 7, fig. 2) is an unneeded replacement name for *Chaetodon unicornis* Forsskål in Niebuhr, 1775, based in part on Forsskål's species and in part on the '*Naseus fronticornis fuscus*' in a manuscript description by Commerson (1767–1771); it is a junior synonym.

Sphyraenidae – Barracudas

Sphyraena barracuda (Edwards in Catesby, 1771)

Forsskål in Niebuhr (1775a: XVI): "37. ESOX *sphyræna*. Arab. *Mughsil* vel *Agam*, vel *Gædd*. [..., Arabic name] Squamis magnis; corpore long. 3 uln.".

Locality: – (Red Sea).

Material: ZMUC P.71369 (1 dry skin) (see Klausewitz & Nielsen 1965: 25).

Remarks: This record is based on the species *Esox sphyraena* (non Linnaeus, 1758); that species is restricted to the Atlantic Ocean including Mediterranean Sea, and does not occur in the Red Sea. Forsskål's specimen was identified by Klausewitz & Nielsen (1965: 25) as *Sphyraena picuda* Bloch & Schneider, 1801, which is a junior synonym of *Sphyraena barracuda* (Edwards in Catesby, 1771).

Sphyraena jello Cuvier in Cuvier & Valenciennes, 1829

Forsskål in Niebuhr (1775a: XVI): "[37. ESOX *sphyræna*] β) *Minor*, squamis parvis. Arab. *Djadd*.".

Type locality: – (Red Sea).

Genus name: *Esox*.

Species/subspecies name (Forsskål): (β); (Fabricius in Niebuhr): *sphyraena minor*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Djadd.

Remarks: In his draft, Forsskål treated this species as an unidentified variety of *Esox sphyraena*, described as 'minor, squamis parvi' with the Arabic name 'Djadd'. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr, however, used the 'minor' as the name for the variety. The name is accompanied by a very brief diagnosis, but recognisable, and therefore would be available as *Esox sphyraena minor* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. Unfortunately, this in an unused senior synonym of *Sphyraena jello* Cuvier in Cuvier & Valenciennes, 1829. The name *Esox sphyraena minor* is rejected here, in accordance with Art. 23.2 and the preamble of ICZN; an application to the International Commission on Zoological Nomenclature will be necessary to retain the name *Sphyraena jello*, which is considered as a valid species.

Trichiuridae – Cutlassfishes

Trichiurus lepturus (Linnaeus, 1758)

Fabricius [ex Forsskål] in Niebuhr (1775a: XIII): "106. CLUPEA a) haumela; polita. *Haumela*.".

Fabricius [ex Forsskål] in Niebuhr (1775a: 72): "106. CLUPEA haumela; *lanceolata, nuda; pinnis V & A. nullis; dorsali per totum dorsum extensa: cauda lineari apterygia*.".

Type locality: "Mochhæ" (Al-Mukhā/Yemen).

Genus name: *Clupea*.

Species name (Forsskål): – (*polita*); (Fabricius in Niebuhr): *haumela*.

Arabic name (Latinised, Forsskål, Fabricius in Niebuhr): Haumela.

Remarks: In his draft, Forsskål used the Arabic name 'haumela' as a substitute for a scientific name possibly to be designated. He did not decide if this was an undescribed species at all. We cannot be certain if the data source for this description was by Forsskål or Niebuhr or both; the description was compiled by Fabricius. Fabricius in Niebuhr described the species as *Clupea haumela* in both the index and text. The use of '*haumela*' as the species name was clearly decided and authored by Fabricius [ex Forsskål]. The name is binominal both in the index and in the text, and accompanied by a diagnosis and description; it would therefore be available as *Clupea haumela* Fabricius [ex Forsskål] in Niebuhr, 1775, the authorship pending a decision of ICZN. However, it is a junior synonym of *Trichiurus lepturus* (Linnaeus, 1758). The species was subsequently misspelled as *Trichiurus hamrela* by Bloch and Schneider (1801: 518; correction to *haumela* on p. 584); this is not an independent species description.

Scombridae – Mackerels and tunas

?Katsuwonus pelamis (Linnaeus, 1758)

Forsskål in Niebuhr (1775a: XVI): "30. SCOMBER d) *thynnus?*. Arab. *Kænad*. In *Mari rubro*. Pinnis spuriis superne & inferne 10; radiis P. D. primæ 16. Longitudo 1 uln.".

Locality: "In *Mari rubro*" (Red Sea).

Remarks: This is a misidentification of the species *Scomber thynnus* (non Linnaeus, 1758); it is most probably based on *Katsuwonus pelamis* (Linnaeus, 1758).

Sarda sarda (Bloch, 1793)

Forsskål in Niebuhr (1775a: XVI): "27. SCOMBER a) *pelamis*. Παλαμίδα. Turc. *Palamít*. lineæ 4. nigræ corporis laterales non manifestæ.".

Locality: "Turc." (Turkey).

Actual Turkish name: Palamut (Fricke et al. 2007: 110).

Remarks: This is a misidentification of the species *Scomber pelamis* (non Linnaeus, 1758); according to the Turkish name, the record is based on *Sarda sarda* (Bloch, 1793), a species which is a migrant regularly found in shallow water, both around İstanbul and İzmir, and which was more common in the past.

Scomber sp.

Forsskål [ex Anonymus] in Niebuhr (1775a: XIX): "[Scomber] *scombrus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This record of *Scomber scombrus* could have been either based on *Scomber colias* Gmelin, 1789, or on *Scomber scombrus* Linnaeus, 1758.

Scomber colias Gmelin, 1789

Forsskål in Niebuhr (1775a: XVI): "28. [SCOMBER] b) *scombrus*. Κολιὸς. Turc. *Kolios-balük*.".

Locality: "Turc." (Turkey).

Actual Turkish name: Kolyoz (Fricke et al. 2007: 110).

Remarks: This is a misidentification of the species *Scomber*

scombrus (non Linnaeus, 1758); according to the Turkish name, the record is based on *Scomber colias* Gmelin, 1789, a species which is regularly found in shallow water, both around İstanbul and İzmir; the Turkish name of *Scomber scombrus* would be 'Uskumru' (FRICKE et al. 2007: 110).

?Thunnus sp.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "SCOMBER *thynnus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Itton.".

Remarks: This record from Malta was based on a name only, and cannot be assigned to species level; it mas have been based on either *Euthynnus alletteratus* (Rafinesque-Schmaltz, 1810), *Orcynopsis unicolor* (Geoffroy Saint-Hilaire, 1817), *Thunnus alalunga* (Bonnaterre, 1788), or *Thunnus thynnus* (Linnaeus, 1758).

Xiphiidae – Swordfishes

Xiphias gladius Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "XIPHIAS *gladius*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Piscis Spat.".

Remarks: The actual vernacular Maltese name of this species is "Pixxispad" (Anonymus 2007b).

Centrolophidae – Medusafishes

Centrolophus niger (Gmelin, 1789)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[CORYPHÆNA] *pompilus*.".

Locality: "Melita" (La Valletta/Malta). Local name: "I Stellara".

Remarks: This record is based on the species *Coryphaena pompilus* Linnaeus, 1758, which is an unused senior synonym of *Centrolophus niger* (Gmelin, 1789); in order to retain the latter name, an application to the International Commission on Zoological Nomenclature will be needed.

Caproidae – Boarfishes

Capros aper (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "ZEUS *aper*.".

Locality: "Melita" (La Valletta/Malta).

Pleuronectiformes – Flatfishes

Pleuronectiformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "PLEURONECTES *limanda*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Pleuronectes limanda* (non Linnaeus, 1758); the latter species is *Limanda limanda* (Linnaeus, 1758), and restricted to the northeastern Atlantic, not occurring south of the Bay of Biscay. FORSSKÅL's Maltese record is unplaceable within the Pleuronectiformes; it may have been based on *Arnoglossus* sp. (family Bothidae).

Pleuronectiformes, incertae sedis

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[PLEURONECTES] *hippoglossus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a misidentification of *Pleuronectes hippoglossus* (non Linnaeus, 1758); the latter species is *Hippoglossus hippoglossus* (Linnaeus, 1758), and restricted to the North Atlantic, not occurring south of the Bay of Biscay. FORSSKÅL's Maltese record is unplaceable within the Pleuronectiformes; it may have been based on *Bothus podas* (family Bothidae).

Citharidae – Largescale flounders

Citharus linguatula (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[PLEURONECTES] *linguatula*.".

Locality: "Melita" (La Valletta/Malta). Local name: "Il Linguada".

Remarks: This species may have been confused with *Arnoglossus imperialis* (Rafinesque-Schmaltz, 1810) or another flatfish species, which have the actual vernacular Maltese name "Lingwata" (Anonymus 2007b).

Scophthalmidae – Turbots

Psetta maxima (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[PLEURONECTES] *psetta*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: This is a name only (nomen nudum), listed as *Pleuronectes psetta* Forsskål [ex Anonymus] in Niebuhr, 1775; neither accompanied by a diagnosis nor an indication, and therefore not available; the record was based on *Psetta maxima* (Linnaeus, 1758).

Scophthalmus rhombus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XIX): "[PLEURONECTES] *rhombus*.".

Locality: "Melita" (La Valletta/Malta).

Pleuronectidae – Righteye flounders

Platichthys luscus (Pallas, 1814)

FORSSKÅL in NIEBUHR (1775a: XV): "12. [PLEURONECTES] b) *papillosus*. Πίσι. Turc. *Pissi balük*. Non facile papillosus; nam radii D. 65. pro 58. V. 6. 7. pro 5. 6. A. 49. pro. 42.".

Locality: – (İstanbul/Turkey, or İzmir/Turkey).

Remarks: This is a misidentification of the species *Pleuronectes papillosus* (non Linnaeus, 1758), which is restricted to the West Atlantic, with the currently used name *Syacium papillosum* (Linnaeus, 1758). FORSSKÅL's Turkish record is based on *Platichthys luscus* (Pallas, 1814), which has the actual Turkish name 'Derepisisi balığı' (FRICKE et al. 2007: 114). The species is common both around İstanbul and İzmir.

Soleidae – Soles

Solea solea (Linnaeus 1758)

FORSSKÅL in NIEBUHR (1775a: XV): "11. PLEURONECTES a) *solea*. Γλόσσα. Turc. *Dil baluk*. …".

Localities: – (İstanbul/Turkey, or İzmir/Turkey); – (Alexandria, Al-Iskandarīyah/Egypt, Mediterranean Sea).

Remarks: This is the Linnaean species *Pleuronectes solea*, which is regularly found in shallow water, both around İstanbul and İzmir.

Balistidae – Triggerfishes

Balistapus undulatus (Park, 1797)

FORSSKÅL in NIEBUHR (1775a: XVII): "[47. BALISTES (*aculeatus*)] b) *minor*, duplici ordine aculeorum; corpore lineis flavis, obliquis.".

Type locality: – (Red Sea) (erroneously listed as 'Izmir and/or Istanbul, Turkey' by ESCHMEYER 2007).

Genus name: *Balistes*.

Species/subspecies name (FORSSKÅL, FABRICIUS in NIEBUHR): *aculeatus minor*.

Remarks: FORSSKÅL described this new variety/subspecies of *Balistes aculeatus* (non Linnaeus, 1758), under the name *Balistes aculeatus minor*; the name was accompanied by a brief diagnosis which is nevertheless characteristic for the species, and the name is available as *Balistes aculeatus minor* Forsskål in Niebuhr, 1775. The name is based on the species which is currently named *Balistapus undulatus* (Park, 1797); *Balistes undulatus* Park, 1797 is a junior synonym of *Balistes aculeatus minor* Forsskål in Niebuhr, 1775. The latter name is here is here rejected according to the preamble and Art. 23.2 of ICZN. In order to preserve stability of nomenclature, and retain the frequently used name *Balistapus undulatus* (Park, 1797), a petition to the International Commission on Zoological Nomenclature is advisable to suppress the name *Balistes aculeatus minor* Forsskål in Niebuhr, 1775.

Balistes capriscus Gmelin, 1789

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[CHÆTODON] *vetula*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: The name '*vetula*' was erroneously listed under the name *Chætodon paru*, but actually belongs to the genus name *Balistes* one line above. This is a misidentification of the Linnaean species *Balistes vetula*; the Maltese record is based on *Balistes capriscus* Linnaeus, 1758.

?Canthidermis macrolepis (Boulenger, 1888)

FORSSKÅL in NIEBUHR (1775a: XVII): "46. BALISTES a) *aculeatus*; *major*: Arab. *Schaaram* [..., Arabic name] Quinque seriebus aculeorum in cauda. Piscis insipidus & foetidus.".

Locality: – (Red Sea).

Remarks: This is a misidentification of the species *Balistes aculeatus* Linnaeus, 1758 [now named *Rhinecanthus aculeatus* (Linnaeus, 1758)], but is a new variety '*Balistes aculeatus major*' (see *Balistapus undulatus*, above, for the other variety, *Balistes aculeatus minor*). The name, however, is not available as *Balistes aculeatus major* Forsskål in Niebuhr, 1775, as the diagnosis is insufficient. Judging from the five series of spines on the caudal peduncle and the large size, the record may have been based on *Canthidermis macrolepis* (Boulenger, 1888).

"*Rhinecanthus assasi* (Forsskål in Niebuhr, 1775)"

FORSSKÅL in NIEBUHR (1775a: XIV): "112. BALISTES VERRUCOSUS. *Azzazi*. [..., Arabic name]".

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: 75): "112. BALISTES ASSASI. DESCR. Parvus: fuscus: ventre albo: *anus* niger, annulo fulvo. ...".

Type locality: "DJIDDÆ" (Jeddah, Juddah/Saudi Arabia).

Genus name: *Balistes*.

Species name (FORSSKÅL): *verrucosus*; (FABRICIUS in NIEBUHR): *assasi*.

Arabic names (Latinised, FORSSKÅL): Azzazi; (FABRICIUS in NIEBUHR): Djemel, Azzazi.

Remarks: In his draft, FORSSKÅL misidentified this species *Balistes verrucosus* (non Linnaeus, 1758) in the index, with 'Azzazi' as the Arabic name, but in the text he used the Arabic name 'azzazi' or 'assasi' as a substitute for a Latin species name possibly to define, in the case the species from Jeddah turned later out to be undescribed. We cannot be certain if the data source for this description was by FORSSKÅL or NIEBUHR or both; the description was compiled by FABRICIUS. FABRICIUS [ex FORSSKÅL] in NIEBUHR described the species in the text as *Balistes assasi*. The use of '*assasi*' as the species name was clearly decided and authored by FABRICIUS [ex FORSSKÅL]. The name is binominal in the text, and accompanied by a description; it would therefore be available as *Balistes assasi* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Rhinecanthus assasi* (Fabricius [ex Forsskål] in Niebuhr, 1775), the authorship pending a decision of ICZN. The species was considered as valid since WALBAUM (1792: 465).

Ostraciidae – Boxfishes

Ostracion cubicus Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XVII): "48. OSTRACION *cubicus*. Arab. *Abu sendûk* [..., Arabic name] Sapidissimus. Solent piscatores ventrem resecare & carnem eximere.".

Locality: – (Red Sea).

Tetrosomus gibbosus (Linnaeus, 1758)

FORSSKÅL in NIEBUHR (1775a: XIV): "113. OSTRACION TURRITUS; dorso gibbo. *Djemel*.".

FORSSKÅL in NIEBUHR (1775a: 75–76): "113. OSTRACION TURRITUS; *superciliis dorsoque spinis solitariis; abdomine spinis utrinque quatuor*.".

Type locality: "MOCHHÆ" (Al-Mukhā/Yemen).

Genus name: *Ostracion*.

Species name (FORSSKÅL, FABRICIUS in NIEBUHR): *turritus*.

Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Djémel.

Remarks: This species was described by both FORSSKÅL and FABRICIUS in NIEBUHR as *Ostracion turritus*. The name is binominal, accompanied by a diagnosis and description, and is available as *Ostracion turritus* Forsskål in Niebuhr, 1775; it was treated as valid by BONNATERRE (1788: 22) and WALBAUM (1792: 476–477). *Ostracion turritus* is a junior synonym of *Ostracion gibbosus* Linnaeus, 1758, with the currently used name *Tetrosomus gibbosus* (Linnaeus, 1758).

?Tetrosomus gibbosus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "OSTRACION *gibbosus*.".

Locality: "Melita" (La Valletta/Malta).

Remarks: The species *Tetrosomus gibbosus* (Linnaeus, 1758) was assumed to have immigrated through the Suez Canal into the southeastern Mediterranean. If FORSSKÅL [ex Anonymus] in NIEBUHR's (1775a) record is correct (and there is no species known in the Mediterranean with which it could be confused), this would mean that the species may have been present in the Mediterranean even before the opening of Suez Canal in 1869.

Tetraodontidae – Puffers

Tetraodontidae, indet.

FABRICIUS [ex FORSSKÅL] in NIEBUHR (1775a: XVII): "51. [TETRAODON] c) *Abu-Kobhla*. Arab. [..., Arabic name]".

Type locality: – (Red Sea).

Genus name: *Tetraodon*.
Species name (FORSSKÅL): –; (FABRICIUS in NIEBUHR): *abu-kobhla*.
Arabic name (Latinised, FORSSKÅL, FABRICIUS in NIEBUHR): Abu kobhla.
Remarks: FORSSKÅL used the Arabic name 'Abu Kobhla' as a substitute for a species which he could not identify; he did not intend to use it as a scientific species name. FABRICIUS [ex FORSSKÅL] in NIEBUHR named the species in the index as *Tetraodon abukobhla* (original spelling of species name 'abu-kobhla'). The name is binominal in the index, but neither accompanied by a diagnosis or a description; it is therefore not available as *Tetraodon abukobhla* Fabricius [ex Forsskål] in Niebuhr, 1775. It is unplaceable within the family Tetraodontidae. ESCHMEYER (2007) erroneously listed the name as '*Tetraodon abukohhla*'.

Tetraodontidae, indet.

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[OSTRACION] *capite testudineo*.".
Locality: "Melita" (La Valletta/Malta).
Remarks: This is not an independent species description with the name *Ostracion capite testudineo* (which would not be available anyway as the name '*Ostracion capite testudineo*' is not binominal, with '*capite testudineo*' being a species name in two words), but is based on the Linnaean species *Tetraodon testudineus*; the species was either deliberately or erroneously placed in the genus *Ostracion*. This was a misidentification; *Sphoeroides testudineus* (Linnaeus, 1758) does not occur in the Mediterranean Sea. The listing is without a diagnosis or indication, and cannot be assigned to genus or species level at present.

Arothron diadematus (Rüppell, 1829)

FORSSKÅL in NIEBUHR (1775a: XVII): "50. [TETRAODON] b) HISPIDUS? Arab. *Edjlis*. [..., Arabic name] Lohajæ. Totus fuscus, areolis contiguis, papillisque albis. ...".
Locality: "Lohajæ" (Al-Luhayya/Yemen).
Material: No FORSSKÅL material extant.
Remarks: This is not an independent species description, but a questionable reference to and a misidentification of the species *Tetraodon hispidus* (non Linnaeus, 1758), a species which is now named *Arothron hispidus* (Linnaeus, 1758). FORSSKÅL's record of the species is based on *Arothron diadematus* (Rüppell, 1829). FORSSKÅL's *Tetraodon hispidus* was also listed in the synonymy and partly forms the basis of *Tetraodon sordidus* Rüppell, 1829 (RÜPPELL 1829: 64), which is a composite species and now treated as a junior synonym of *Arothron immaculatus* (Bloch & Schneider, 1801) (ESCHMEYER 2007).

Arothron perspicillaris (Rüppell, 1829)

FORSSKÅL in NIEBUHR (1775a: XVII): "49. TETRAODON a) OCELLATUS? Arab. *Drimme* vel *Kavvat*. Lineæ flavæ circa pinnas Pect. Corpus supra fuscum, maculis cæruleo-albidis. ...".
Locality: – (Red Sea).
Material: ZMUC P.89123 (see KLAUSEWITZ & NIELSEN 1965: 26, pl. 38).
Remarks: This is not an independent species description, but a questionable reference to and a misidentification of the species *Tetraodon ocellatus* (non Linnaeus, 1758), a species which is now named *Takifugu ocellatus* (Linnaeus), and is restricted to East Asia. FORSSKÅL's record of the species is based on *Arothron perspicillaris* (Rüppell, 1829) according to KLAUSEWITZ & NIELSEN (1965: 26). This species is often treated as a valid subspecies of *Arothron hispidus* (Linnaeus, 1758).

Lagocephalus lagocephalus (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[OSTRACION] *lagocephalus*.".
Locality: "Melita" (La Valletta/Malta).
Remarks: This is not an independent species description with the name *Ostracion lagocephalus*, but is based on the Linnaean species *Tetraodon lagocephalus*; the species was either deliberately or erroneously placed in the genus *Ostracion*. The species is valid, and the currently used name is *Lagocephalus lagocephalus* (Linnaeus, 1758).

Tetraodon lineatus Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XIV): "114. TETRAODON, *lineatus*. Fahaka.".
FORSSKÅL in NIEBUHR (1775a: 76): "114. TETRAODON LINEATUS. Arab. *Fahaka*.".
Locality: "E *Nilo*" (Nile/Egypt).
Remarks: This is a record of the Linnaean species *Tetraodon lineatus*, which is regularly found in River Nile. This species was subsequently named *Tetrodon physa* Geoffroy Saint-Hilaire, 1809 (GEOFFROY SAINT-HILAIRE 1809: 19–37, pl. 1, fig. 1, pl. 2), which is a junior synonym of *Tetraodon lineatus*.

D i o d o n t i d a e – Porcupinefishes

Diodon hystrix Linnaeus, 1758

FORSSKÅL in NIEBUHR (1775a: XVII): "52. DIODON *hystrix*. Arab. *Schokiæ* [..., Arabic name] vel *Abu mechajat*. Maculatus; in ventre duæ venæ venenatæ.".
Locality: – (Red Sea).

Diodon hystrix Linnaeus, 1758

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[OSTRACION] *hystrix*.".
Locality: "Melita" (La Valletta/Malta). Local Maltese name: "Il Rizza".
Remarks: This is not an independent species description with the name *Ostracion hystrix*, but is based on the Linnaean species *Diodon hystrix*; the species was either deliberately or erroneously placed in the genus *Ostracion*. The species is valid, and the currently used name is *Diodon hystrix* Linnaeus, 1758.

M o l i d a e – Molas

Mola mola (Linnaeus, 1758)

FORSSKÅL [ex Anonymus] in NIEBUHR (1775a: XVIII): "[OSTRACION] *mola*.".
Locality: "Melita" (La Valletta/Malta). Local Maltese name: "I Kamar".
Remarks: This is not an independent species description with the name *Ostracion mola*, but is based on the Linnaean species *Tetraodon mola*; the species was either deliberately or erroneously placed in the genus *Ostracion*. The species is valid, and the currently used name is *Mola mola* (Linnaeus, 1758).

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Valid taxa are printed in **bold face**. 'ä' and 'æ' are listed as 'ae', 'ö' as 'oe', and 'ü' as 'ue'.

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Manuscript received: 13.VIII.2007, accepted: 9.XI.2007.

Review of the genus *Parablennius* Miranda-Ribeiro from Australia and New Caledonia (Pisces: Blenniidae: Salariinae)

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Abstract

The blenniid fishes of the genus *Parablennius* of Australia and New Caledonia (excluding Norfolk Island) are reviewed. *Parablennius tasmanianus* (Richardson, 1842) from southern Australia, *P. intermedius* (Ogilby, 1915) from eastern Australia and New Caledonia, and *P. postoculomaculatus* Bath & Hutchins, 1986 from Western Australia are valid species in the area. *Parablennius tasmanianus caledoniensis* Bath, 1989 **n. syn.** is a junior synonym of *P. intermedius*. One specimen questionably conspecific with *Parablennius intermedius* is known from the Solomon Islands. The colouration of freshly collected specimens is redescribed. A key to the species of the complex is presented.

Keywords: Blennies, Blenniidae, *Parablennius*, Australia, New Caledonia.

Zusammenfassung

Die Schleimfische der Gattung *Parablennius* aus Australien und Neukaledonien (außer Norfolk Island) werden überarbeitet. Gültige Arten des Gebietes sind *Parablennius tasmanianus* (Richardson, 1842) aus dem südlichen Australien, *P. intermedius* (Ogilby, 1915) aus Ostaustralien und Neukaledonien sowie *P. postoculomaculatus* Bath & Hutchins, 1986 aus Westaustralien. *Parablennius tasmanianus caledoniensis* Bath, 1989 **n. syn.** ist ein jüngeres Synonym von *P. intermedius*. Ein möglicherweise zu *Parablennius intermedius* gehörendes Exemplar ist von den Salomonen bekannt. Das Farbmuster frisch gesammelter Exemplare wird detailliert beschrieben. Ein Bestimmungsschlüssel unterscheidet die Arten des Artenkomplexes.

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1 Introduction

The Australian and New Zealand species of the salariine blennies of the genus *Parablennius* were revised by Bath & Hutchins (1986), who distinguished five different taxa, *P. laticlavius* (Griffin, 1926) from New Zealand, *P. serratolineatus* Bath & Hutchins, 1986 from Norfolk Island, and *P. tasmanianus* (Richardson, 1842) including three subspecies, *P. tasmanianus tasmanianus* from South Australia, Tasmania, Victoria and southern New South Wales, *P. tasmanianus intermedius* (Ogilby, 1915) from Queensland and New South Wales, and *P. tasmanianus postoculomaculatus* from Western Australia. Bath (1989) described another subspecies, *P. tasmanianus caledoniensis* from Nouméa area, New Caledonia. Subsequently, several authors recognized the subspecies as species (e. g. Hutchins & Swainston 1986, Hutchins 1994, Kuiter 1996, Griffiths 2003).

Head and body colouration, as well as head lateral line pores, are important characters for distinguishing the species in the *Parablennius tasmanianus* complex. An extended fixation of specimens in formalin, or the effects of light over a longer period of time, may dramatically fade fresh colouration. Both Bath & Hutchins (1986) and Bath (1989) examined several older specimens, many of which were faded. When fresh material became available, it was considered important to re-examine the taxonomy of the group.

Acknowledgements

I would like to thank R. Fricke (SMNS, Stuttgart) for supporting the present study, and J. Reibnitz and H.-P. Tschorsnig (Stuttgart) for improving the figures.

2 Methods and materials

2.1 Methods

Methods follow BATH & HUTCHINS (1986). Species are diagnosed; the colour of freshly collected specimens which were preserved in alcohol is redescribed in detail. Standard length is abbreviated as SL, total length as TL, length of supraorbital tentacle as ST. Head lateral line pore numbers refer to the total count of pores on both sides of the head.

2.2 Materials

Specimens are deposited in the following collections (in general, acronyms follow LEVITON et al. 1985 and LEVITON & GIBBS 1988, but with additions and amendments):

AMS	The Australian Museum, Sydney, Australia
ANSP	Academy of Natural Sciences of Philadelphia, U.S.A.
BMNH	The Natural History Museum, London, U.K. [formerly British Museum (Natural History)]
NMW	Naturhistorisches Museum, Wien, Austria
QM	Queensland Museum, Brisbane, Australia
SB	Fish Collection BATH, Pirmasens, Germany
SMF	Forschungsinstitut Senckenberg, Frankfurt/Main, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.
WAM	Western Australian Museum, Perth, Australia

3 Species accounts

3.1 *Parablennius tasmanianus* (Richardson, 1842) (Figs. 1–2)

Blennius tasmanius Richardson, 1839: RICHARDSON 1839: 99 (nomen nudum; Port Arthur/Tasmania, Australia).

Blennius tasmanianus Richardson, 1842: RICHARDSON 1842: 129–130 (Port Arthur/Tasmania, Australia; holotype: BMNH 1855.9.19.714). – GÜNTHER 1861: 214 (Van Diemen's Land/Tasmania, Australia). – FOWLER 1908: 444 (in comparison with *B. victoriae*). – WAITE 1921: 150, fig. (South Australia). – MCCULLOCH 1929: 346 (Tasmania). – WHITLEY 1929: 65 (Government House jetty/Hobart, Tasmania; abundant on 1 Nov. 1881 according to R. M. JOHNSTON's notes).

Bl[ennius] maoricus Kner, 1864: KNER 1864: 503 (Auckland, New Zealand, undoubtedly erroneous; see discussion; holotype: NMW 78544).

Blennius victoriae Fowler, 1908: FOWLER 1908: 442–444, fig. 10 (Victoria/Australia; holotype: ANSP 33128). – MCCULLOCH 1929: 346 (Victoria/Australia).

Pictiblennius tasmanianus: WHITLEY 1930: 19 (new generic association). – BATH 1977: 204 (revision; southeastern Australia, synonymy). – SCOTT et al. 1974: 277, fig. (South Australia). – LAST et al. 1983: 442, fig. (Tasmania, Victoria, New South Wales and South Australia). – GRANT 1987: 333, fig. 712 (New South Wales, Victoria, Tasmania/Australia; etc.).

Pictiblennius victoriae: BATH 1977: 205 (revision; Victoria/Australia).

Parablennius tasmanianus: BATH 1982: 219 (generic association). – BATH 1990: 66 (in key; Tasmania, SE Australia). – HUTCHINS & SWAINSTON 1986: 94, 139, fig. 526 (Australia). – KUITER 1996: 326, fig. (Australia). – YEARSLEY et al. 1997: Code 37 408002 (Australia; CAAB Code). – WATSON & MISKIEWICZ in NEIRA et al. 1998: 378–379, figs. A–D (central New South Wales southward, Victoria, Tasmania/Australia; etc.; larvae). – TURNER & NORMAN 1998: 152 (Wilson's Promontory/Victoria, Australia; in checklist).

Parablennius tasmanianus tasmanianus: BATH & HUTCHINS 1986: 172–179, figs. 4–8, 9a–k, 10a–l (revision; southeastern Australia). – BATH 1996: 91 (in checklist of tribe Parablenniini).

Material

Total: 74 specimens.

Australia, South Australia: AMS I.20160-028, 1 female, Vivonne Bay, Kangaroo Island, 35°58'S 137°10'E, 2 Mar. 1978; AMS I.20168-022, 1 male, Hanson Bay, Kangaroo Island, 6 Mar. 1978; AMS I.20166-016, 1 male, Stokes Bay, Kangaroo Island, 5 Mar. 1978; WAM P.27141-004, 1 male, Port James, east of Ceduna, 32°S 133°E, 11 Apr. 1981. – **Australia, Tasmania**: AMS I.17549-004, 1 male, Oyster Cove, 43°07'S 147°15'E, 1 Dec. 1972; AMS I.17585-003, 2 males and 3 females, Boat Harbour, 9 Dec. 1972; AMS I.18716-001, 1 male, Hobart, 42°54'S 147°18'E, 15 Feb. 1976; AMS I.20075-006, 2 males and 3 females, King Island, Naracoopa, 39°55'S 144°08'E, Dec. 1977; AMS I.20094-004, 4 males and 3 females, Killiecrankie Bay, Flinders Island, 6 Jan. 1978; SB uncat., 1 male, Granville Harbour, 12 Dec. 1972; SMNS 6054, 1 specimen, Stanley, Rocky Cape, northwestern Tasmania, 40°52'S 145°25'E, D. F. HOESE, 11 Dec. 1972; WAM P.27556-002, 2 males and 3 females, Saint Helen's Point, 41°16'S 148°20'E, 24 Feb. 1982; WAM P.27568-008, 4 males and 1 female, Western Bay, 8 Mar. 1982. – **Australia, Victoria**: AMS I.16968-001, 3 males, Cape Conran, 37°51'S 148°42'E, 13 Mar. 1972; AMS I.16979-002, 7 males and 2 females, Walkerville, 17 Mar. 1972; AMS I.16981-002, 1 male and 1 female, and AMS I.16982-003, 1 male and 4 females, Bell's Beach, south of Geelong, 38°10'S 144°26'E, 18 Mar. 1972; AMS I.16987-005, 2 males and 1 female, estuary at Petersborough, 38°36'S 142°55'E, 21 Mar. 1972; AMS I.18470-009, 2 males and 3 females, Children's Cove, east of Warmanbool, 22 Mar. 1972. – **Australia, New South Wales**: AMS I.16502-004, 1 female, Madgee River, 26 Apr. 1967; AMS I.16966-003, 1 female, off Twofold Bay, at Boydtown, 12 Mar. 1972; AMS I.28727-005, 6 males and 1 female, Cape Howe, 37°15'15"S 150°00'50"E, AMS party, 5 Apr. 1989; SMNS 21387, 3 specimens, Cape Dromedary, 500 m southeast of Mystery Bay, 10 km south of Narooma, 36°18'14"S 150°08'13"E, 0–2.5 m depth, R. FRICKE, 11 July 1999. – **Locality unknown** (erroneously recorded from New Zealand): NMW 78544, 1 male, holotype of *Blennius maoricus* Kner, 1864, allegedly from Auckland, North Island, New Zealand.

Diagnosis

A species of *Parablennius* usually with 18–19 segmented dorsal fin rays and 19–20 segmented anal fin rays; with the supraorbital tentacle in both sexes consisting of a large, stout main tentacle with a row of lateral branches at its median side; with 102–304 pores of the head lateral line system (mean 178.4); with the side of the head usually with two brown bands, extending down from the lower margin of the orbit; usually without an angular mark on the lower side of the head; sides of body with six groups of spots in its upper half, which fade at a larger body size and may disappear completely in large adults.

Colour description

Colour in alcohol. Body colouration: Head and body light yellowish brown to greyish brown. Head in most specimens in the postorbital region with a dark spot which is bordered dorsally by a light, dark-edged stripe and anteriorly by a narrow dark stripe, situated a little lower than the eye. Sides of head in most specimens with two brown bands. The anterior band is reaching from the lower anterior margin of the orbit down to the median upper margin of the upper lip, often extending on the upper lip; the posterior band extending from the lower posterior margin of the orbit to the posterior end of the maxilla, sometimes reaching the branchiostegal membrane.

Some specimens, collected throughout the distribution range of the species, have irregular blotches on the preopercle, opercle, and pectoral fin base. These blotches are usually faint, and are half diameter of pupil. The remainder of the sides of the head is usually a little darker than the body ground colouration. The head of males during courtship is plain dark greyish.

A few specimens have a complete angular brown streak on the lower sides of the head, most others are lacking this streak. Very rarely a pair of such streaks is observed; in which case, the anterior streak extends posteroventrally from below the posterior margin of the maxilla, and the posterior streak extends obliquely across the branchiostegal rays. The anterior pair of streaks, however, does not join in the middle to a complete angular marking.

The body colour is variable, and changes with age and body size. Specimens usually have a pattern of brown blotches, which become faint with age, and may disappear completely in large adults. Many specimens have six groups of large, brown to blackish brown blotches along the sides of the body; these may be confined to the upper one-third of the body, or may extend ventrally to the lateral line. In the latter case, the blotches in the upper one-third are significantly larger than those close to the lateral line. Usually, the largest blotches are found below the dorsal fin base; they may extend on the basal membranes of the dorsal fin. The anteriormost blotches, below the 3rd or 4th dorsal fin spines, are usually confluent, forming an oblique, broad, irregular cross-bar. The 3rd to 5th groups of blotches are usually most distinct. The 6th group is often very faint or may be lacking completely. The blotches above the lateral line, if present, are usually situated a little further caudally than the corresponding upper groups of blotches. Many specimens have very small, additional light or dark brown spots on the head and body, sometimes only extending across the anterior one-third of the body, in other cases reaching the caudal peduncle. If these additional spots are present, those on the head are smaller and paler than those on the body. The additional small spots are present in specimens from different areas throughout the distribution of the species.

The dorsal fin may be plain yellowish or light grey, sometimes with a darker distal margin. Few specimens may have irregular blackish brown spots on the basal parts of the fin membranes. Males with an oval or triangular dark greyish or black blotch on the distal one-third of the first inter-spinous membrane of the dorsal fin. Rarely, the second membrane has a similar, but paler blotch. Females have a very pale blotch on the first inter-spinous membrane, or lack the blotch entirely.

The anal fin is light grey to grey, with a darker distal margin. The tips of the fin rays are whitish. Pectoral fins plain grey. Pelvic fins whitish, brownish or greyish brown. Caudal fin plain light grey or yellowish brown.

Colour in life [based on a specimen from Tasmania, photo by D. Harasdi, published in the internet by Scuba Equipment U.S.A. Marine Species Gallery, http://www.scuba-equipment-usa.com/marine/JUL04/Tasmanian_Blenny(Parablennius_tasmanianus).html]. Head rose, anterior body cream, posterior body and back yellowish; supraorbital tentacle blackish; streaks and blotches on head and body pale brown; dorsal, caudal and pectoral fin rays yellowish; grey blotch on 1st membrane of dorsal fin; pelvic fins white.

Distribution

The new species is known from South Australia, Tasmania, Victoria and southern New South Wales (Fig. 3); it is found on rocky reefs and tidal rockpools in shallow water, but also enters adjacent sand and shell rubble bottom.

Remarks

The species was treated by Bath & Hutchins (1986) as the nominal subspecies of *Parablennius tasmanianus*. It is now raised to species level (see discussion under 5).

Blennius maoricus was originally described by Kner (1864: 503) from Auckland, New Zealand. The holotype, NMW 78544, is extant, and is evidently not the New Zealand species *Parablennius laticlavius*, but most probably a specimen of *Parablennius tasmanianus*. The type locality of *Blennius maoricus* was most probably incorrect; the specimen may have been collected in Tasmania. *Blennius maoricus* is a junior synonym of *Parablennius tasmanianus*.

3.2 *Parablennius intermedius* (Ogilby, 1915) (Figs. 4–7)

a) Eastern Australian populations

Blennius tasmanianus (non Richardson, 1842): Günther 1880: 28 (Port Jackson/New South Wales, Australia).

Blennius castaneus Macleay, 1881: Macleay 1881: 5 (Port Jackson/Sydney Harbour, New South Wales, Australia; holotype: AMS I.16407-001; name invalid due to primary homonymy with *Blennius castaneus* Castelnau, 1861).

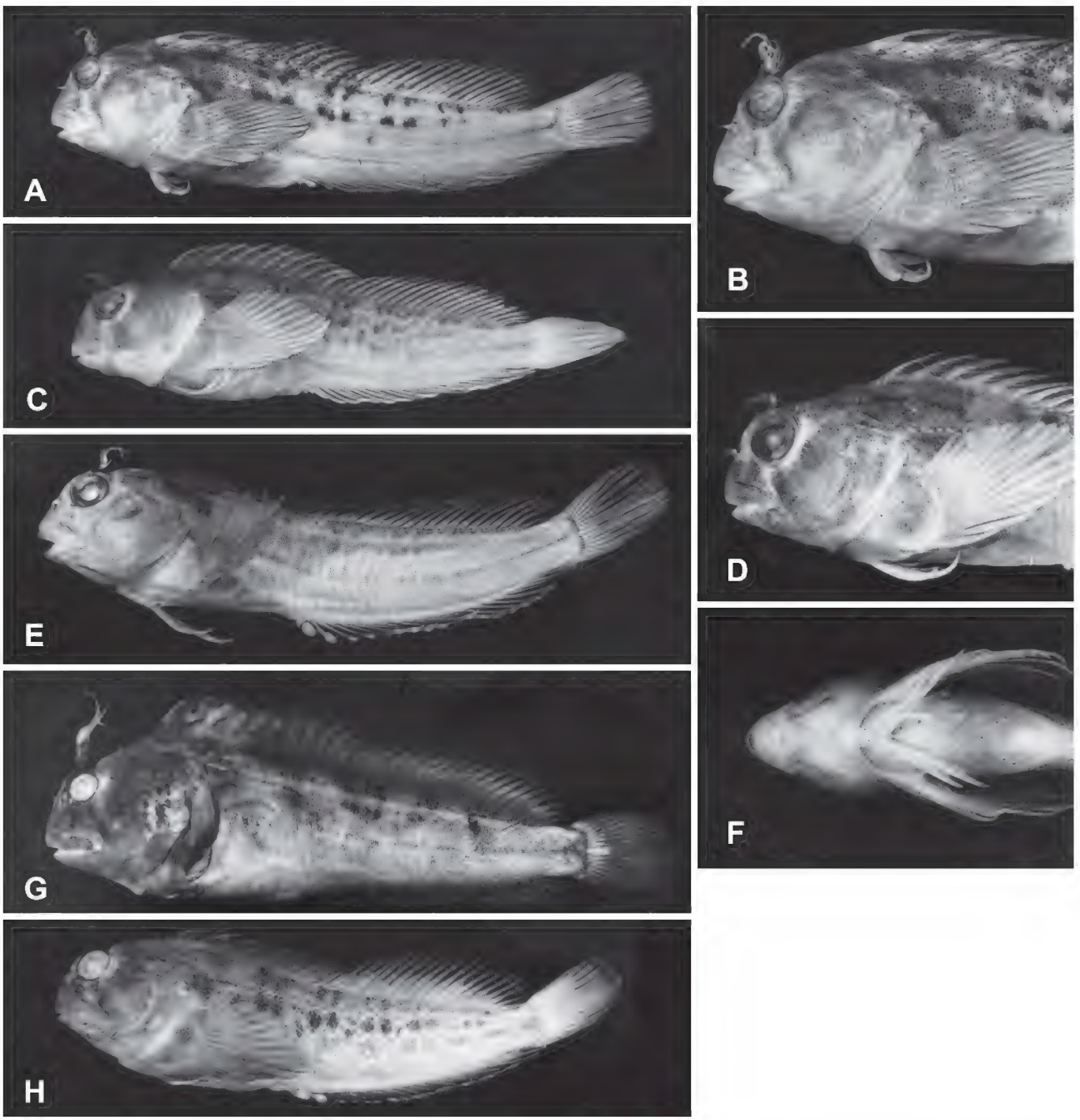

Fig. 1. *Parablennius tasmanianus* (Richardson, 1842), Australia. – **A–B**. WAM P.27556-002, male, 71.1 mm SL, Saint-Helen's Point, Tasmania, lateral view (A), enlarged lateral view of head (B). **C–D**. AMS I.16979-002, male, 39.3 mm SL, Walkerville South, Victoria, lateral view (C), enlarged lateral view of head (D). **E–F**. AMS I.18470-009, male, 44.5 mm SL, Robe, South Australia, lateral view (E), enlarged lateral view of head (F). **G**. AMS I.18716-001, male, 77.7 mm SL, Hobart, Tasmania, lateral view. **H**. AMS I.20094-004, male, 54.1 mm SL, Flinders Island, Tasmania, lateral view.

Blennius intermedius Ogilby, 1915: Ogilby 1915: 127 (Darnley Island/Queensland, Australia; holotype: QM I.1450). – McCulloch & Whitley 1925: 173 (Darnley Island, Queensland/Australia). – McCulloch 1929: 346 (Queensland/Australia).

Pictiblennius intermedius: Whitley 1930: 19 (type species of new genus description). – Bath 1977: 202 (revision; Darnley Island, Queensland).

Pictiblennius iredalei Whitley, 1931: Whitley 1931: 323 (replacement name for *Blennius castaneus* Macleay, 1881; holotype: AMS I.16407-001).

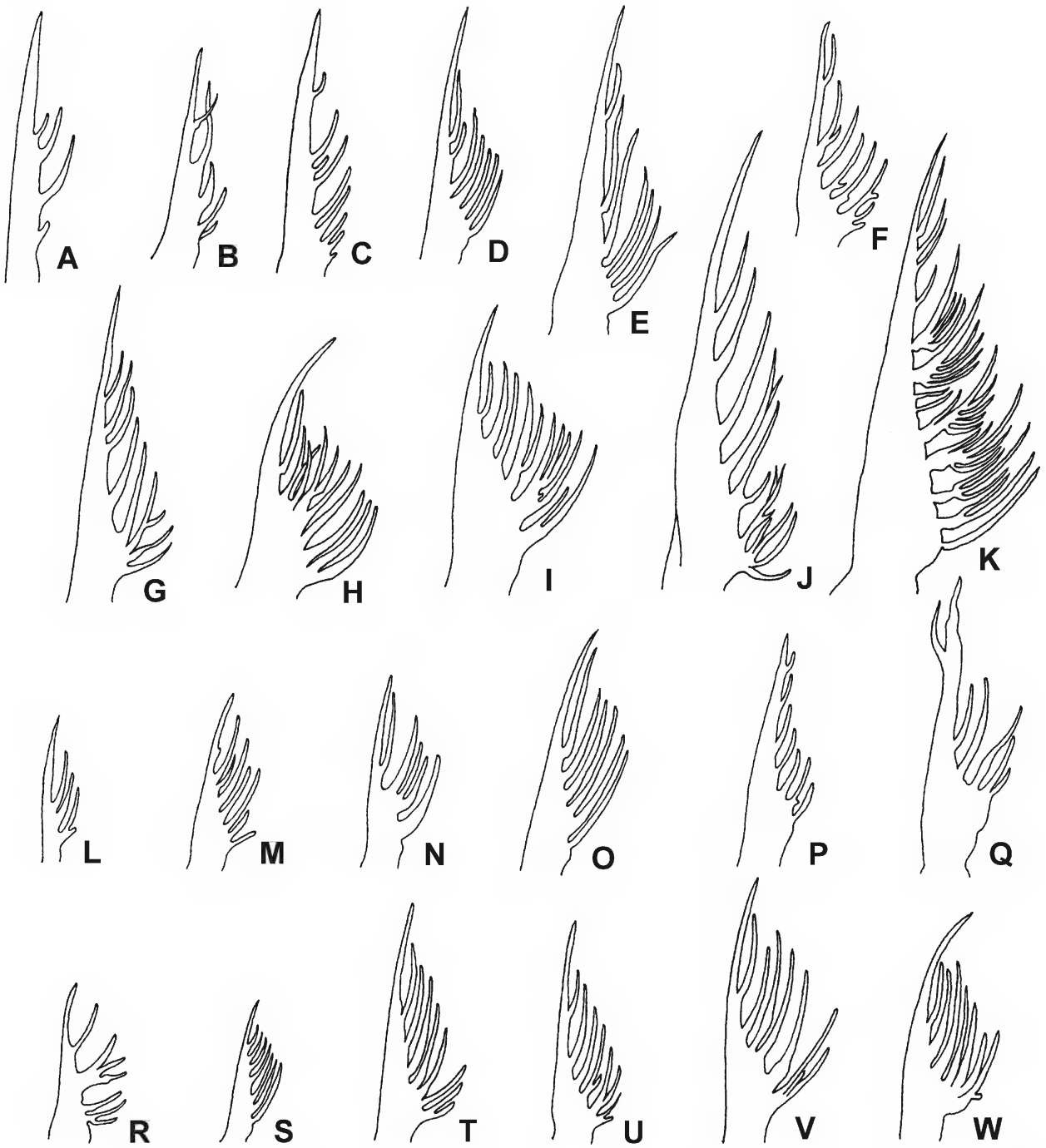

Fig. 2. *Parablennius tasmanianus* (Richardson, 1842), Australia, right supraorbital tentacle of males (A–K) and females (L–W). – **A**. Oyster Cove, Tasmania, 46.5 mm TL, 4.2 mm ST. **B**. Granville Harbour, Tasmania, 50.0 mm TL, 5.0 mm ST. **C**. Petersborough, Victoria, 36.8 mm TL, 4.1 mm ST. **D**. Robe, South Australia, 53.5 mm TL, 4.3 mm ST. **E**. Stokes Bay, Kangaroo Island, South Australia, 93.5 mm TL, 8.0 mm ST. **F**. King Island, 54.3 mm TL, 4.1 mm ST. **G**. Flinders Island, Tasmania, 64.4 mm TL, 7.6 mm ST. **H**. Saint Helen's Point, Tasmania, 83.2 mm TL, 6.7 mm ST. **I**. Port James, South Australia, 113.0 mm TL, 6.0 mm ST. **J**. Bell's Beach, Tasmania, 82.0 mm TL, 6.8 mm ST. **K**. Hobart, Tasmania, 91.4 mm TL, 9.9 mm ST. – **L**. Vivonne Bay, Kangaroo Island, 40.2 mm TL, 2.3 mm ST. **M**. Robe, South Australia, 46.3 mm TL, 1.9 mm ST. **N**. Robe, South Australia, 53.3 mm TL, 2.4 mm ST. **O**. Children's Cove, Victoria, 64.4 mm TL, 3.4 mm ST. **P**. Petersborough, Victoria, 40.5 mm TL, 3.0 mm ST. **Q**. Madgee River, New South Wales, 46.0 mm TL, 4.0 mm ST. **R**. King Island, 70.6 mm TL, 2.8 mm ST. **S**. Flinders Island, Tasmania, 53.8 mm TL, 1.8 mm ST. **T**. Bell's Beach, Victoria, 60.9 mm TL, 3.8 mm ST. **U**. Western Bay, Tasmania, 66.0 mm TL, 3.6 mm ST. **V**. Boat Harbour, Tasmania, 70.3 mm TL, 4.2 mm ST. **W**. Saint Helen's Point, Tasmania, 85.8 mm TL, 5.8 mm ST.

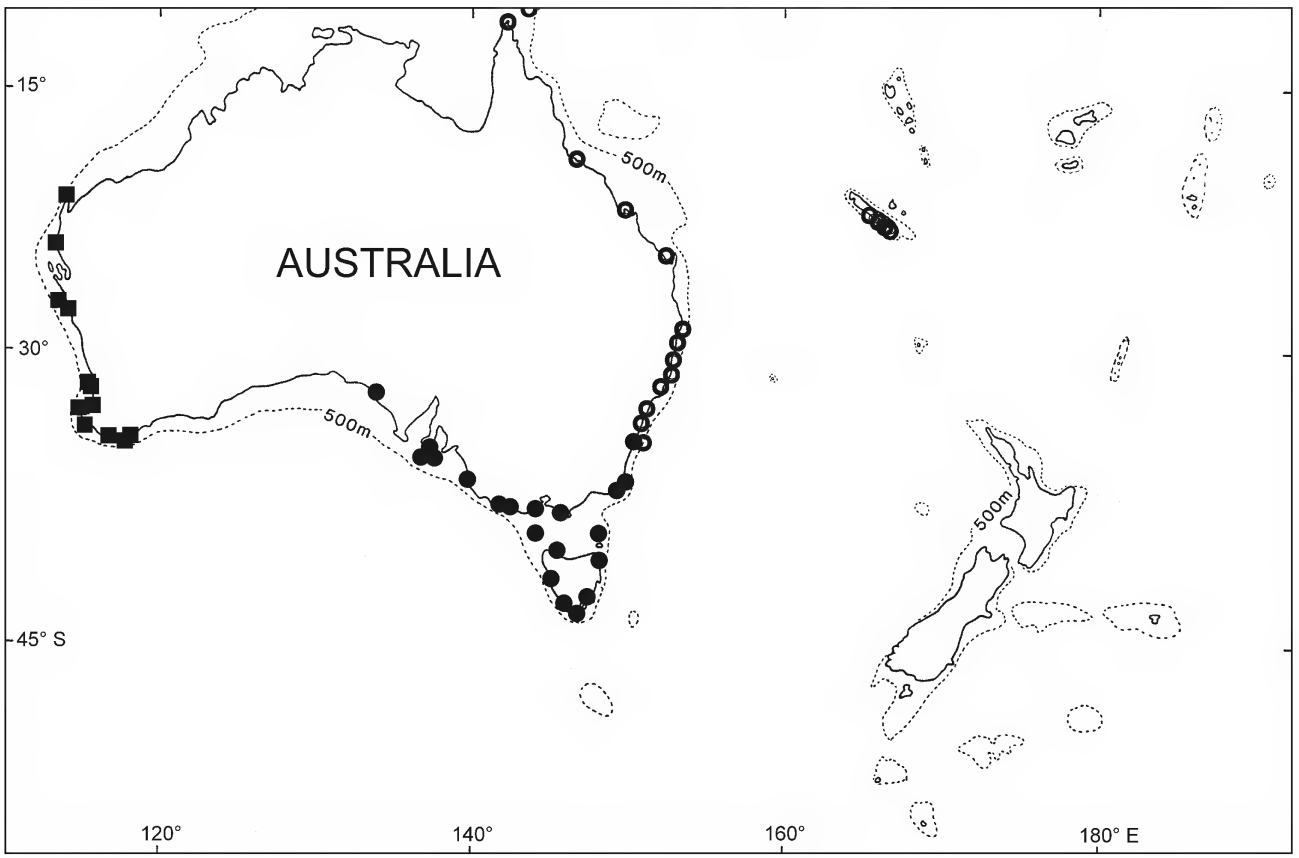

Fig. 3. Geographical distribution of the Australian and New Caledonian species of *Parablennius*. – *P. intermedius* (○), *P. tasmanianus* (●), *P. postoculomaculatus* (■).

Parablennius tasmanianus intermedius: Bath & Hutchins 1986: 179–187, figs. 12–15, 22 a–l, 23a–n (revision; eastern Australia). – Bath 1990: 66 (in key; eastern Australia). – Johnson 1999: 746 (Moreton Bay; in checklist). – Springer 2001: 3545 (W Pacific; in checklist).

Parablennius intermedius: Hutchins & Swainston 1986: 94, 139, fig. 527 (Australia). – Kuiter 1996: 326, fig. (Australia). – Yearsley et al. 1997: Code 37 408067 (Australia; CAAB Code). – Watson & Miskiewicz in Neira et al. 1998: 374–375, figs. A–E (Cape York/Queensland southward, New South Wales, Cape Conran/Victoria northward/Australia; etc.; larvae). – Coleman & Connell 2001: 236 (Sydney Harbour/New South Wales, Australia). – Silberschneider & Booth 2001: 198 (northern beaches, Sydney/New South Wales, Australia). – Griffiths 2003: 167 (rock pools; Bass Point, Bellambi Point, Caravan Point/S New South Wales, Australia).

Parablennius tasminianus intermedius: Bath 1996: 91 (name in checklist of tribe Parablenniini).

Material

Total: 123 specimens.

Australia, Queensland: AMS I.7096–I.7103, 6 males and 6 females, Capricorn Group, Masthead Island, 23°30'S 151°14'E, 8 Feb. 1905; AMS I.20776-037, 2 males and 3 females, Cape York, False Oxford Ness Point, 10°42'S 142°32'E, 18 Feb. 1979; AMS I.20904-005, 2 males, Cape Fergusson, 4 Feb. 1979; QM I.1450, holotype of *Blennius intermedius* Ogilby, female, Darnley Island, ca. 9°35'S ca. 143°46'E; WAM P.27064-011, 3 males and 2 females, Bargara, Kelly's Beach, 24°49'S 152°29'E, H. Bath, 2 Dec. 1980. – **Australia, New South Wales**: AMS IA.5926, 1 male, Bottle and Glass Rocks, Port Jackson, 33°55'S 151°10'E; AMS IA.8051, 1 male, off Balmoral Beach, Port Jackson; AMS I.16236-003, 3 males and 2 females, Long Reef, Dee Why, 12 Feb. 1972; AMS I.16250-019, 3 males and 2 females, Seal Rocks, 27 May 1972; AMS I.16407-001, holotype of *Blennius castaneus* Macleay and *Pictiblennius iredalei* Whitley, female, Port Jackson; AMS I.16467-006, 5 males and 2 females, Minnie Waters, 14 Feb. 1965; AMS I.16970-004, 2 males and 2 females, Nullica Bay, Boydtown, 13 Mar. 1972; AMS I.40838-015, 6 males and 2 females, Sydney Harbour, Gore Cove, AMS team, 3 May 2001; AMS I.40869-005, 1 male and 2 females, Sydney Cove, north end of overseas terminal, 33°51.45'S 151°12.33'E, AMS team, 24 May 2001; AMS I.41262-019, 6 males, south end of Lennox Head, 28°49.36'S 153°36.36'E, A. Gill, M. McGrouther & J. Pogonoski, 20 Mar. 2002; AMS I.41268-015, 1 female, Broken Head Point, 28°42.45'S 153°37.13'E, M. McGrouther, K. Parkinson & J. Pogonoski, 21 Mar. 2002; AMS I.41273-018, 4 males and 4 females, Hastings Point, Cudgera Creek, 28°21.69'S 153°34.58'E, A. Gill, M. McGrouther & J. Pogonoski, 22 Mar. 2002; AMS I.41874-016, 5 males and 7 females, Hastings Point, Cudgera Creek, 28°21.63'S 153°34.53'E, M. McGrouther, A. Gill & J. Pogonoski, 11 Dec. 2002; AMS I.41877-029, 3 males and 4 females, Spooky Point, Angurie, 29°28.73'S 153°32.83'E, 12 Dec. 2002; SB uncat., 1 male, Seal

Rocks, 9 May 1971, SB uncat., 1 female, Maroubra Beach, Sydney, 23 Mar. 1967; SMNS 14760, 1 specimen, Red Head, 1 km east of Bendalong, 13 km eastnortheast of Ulladulla, 35°14'55"S 150°32'39"E, 0–3 m depth, R. Fricke & T. Trnski, 12 May 1993; SMNS 21407, 10 specimens, Wagonga Head, 1 km east of Narooma, deep tidal pool at outer base of southern harbour jetty, 36°13'02"S 150°07'55"E, 0–3 m depth, R. Fricke, 11 July 1999; WAM P.17112-006, 1 male, Shelley Point, Summercloud Bay, 9 Feb. 1981. – **Australia, Australian Capital Territory**: AMS I.15330-018, 7 males and 3 females, Jervis Bay, Chinaman's Beach, 3 Jan. 1969; AMS I.15912-029, 3 males and 2 females, Jervis Bay, Cabbagetree Point, 17 Dec. 1970. – ?**Solomon Islands**: CAS 66848, 1 specimen, New Georgia, outer reef of Wana-Wana Island and Blackett Straits, W. M. Chapman & H. Cheyne, 25 June 1944.

b) New Caledonian populations

Parablennius tasmanianus caledoniensis Bath, 1989: Bath 1989: 293–300, figs. 1–4, 5a–e, 6a–b, 9 (Ducos Peninsula, Nouméa, New Caledonia; holotype: USNM 195795). – Bath 1990: 66 (in key; New Caledonia). – Bath 1996: 91 (name in checklist of tribe Parablenniini). – Springer 2001: 3545 (W Pacific; in checklist).

Parablennius tasmanianus (non Richardson, 1842): Fricke & Kulbicki 2006: 347 (New Caledonia; in checklist).

Material

Total: 17 specimens.

New Caledonia, Grande Terre Group, Province Sud: SMF 18007, 1 paratype of *Parablennius tasmanianus caledoniensis* Bath, male, same data as the holotype; SMNS 22624, 4 specimens, and SMNS 22834, 4 specimens, Baie de Gouaro, at Roche Percée, 20 m east of rock, 9 km southwest of Bourail, southwest coast, 21°36'29"S 165°27'21"E, 0–4 m depth, R. Fricke, 15 May 2000; SMNS 23045, 4 males, Île Nou/Nou Island, 200 m west of Pointe Kongou, at lighthouse, 6.5 km westnorthwest of Nouméa, southern entrance of Grande Rade, southwest coast, 22°14'54"S 166°23'13"E, 0–2 m depth, R. Fricke, 24 Nov. 2000; USNM 195794, 1 paratype of *Parablennius tasmanianus caledoniensis* Bath, female, Nouméa Harbour, W. M. Chapman & H. Cheyne, 25 Mar. 1944; USNM 195795, holotype of *Parablennius tasmanianus caledoniensis* Bath, male, Nouméa, Ducos Peninsula, W. M. Chapman & H. Cheyne, 8 Apr. 1944; USNM 195796, 1 paratype of *Parablennius tasmanianus caledoniensis* Bath, female, Nouméa, tide pool near Camp Goetige, W. M. Chapman & H. Cheyne, 28 Mar. 1944; USNM 280244, 1 paratype of *Parablennius tasmanianus caledoniensis* Bath, Nouméa, W. M. Chapman & H. Cheyne, USNM 313669, 1 male and 1 female, Bourail, Roche Percée, R. Snider, 24 Sep. 1964.

Diagnosis

A species of *Parablennius* usually with 16–17 segmented dorsal fin rays and 18–19 segmented anal fin rays. Eastern Australian populations with the supraorbital tentacle in both sexes consisting of a hand-shaped, basally broad main tentacle with side branches of irregular length, but the lateral branch usually not longer or broader than the others; New Caledonian populations with the supraorbital tentacle in both sexes with a longer, stouter main tentacle and usually less than five side branches; eastern Australian populations with 92–190 pores of the head lateral line system (mean 144.1), New Caledonian populations 108–139 (mean 126.6); the side of the head in males with vertical, narrow bands extending on the upper lip; cheeks, opercle and pectoral fin base with dark blotches; lower side of head in New Caledonian populations with dark angular mark; upper sides of body with dark or blackish brown blotches with clearly confined margins, extending in three longitudinal rows of six groups of blotches each, except for a longitudinal blotch in the middle of the caudal peduncle.

Colour description

a) Eastern Australian populations (Figs. 4–5)

Colour in alcohol. Head and body light brown to brown. Postorbital region with a blotch of eye size in various shapes, situated a little lower than the eye. The blotch is usually medium to dark brown, with a narrow black margin anteriorly, sometimes also posteriorly, occasionally bordered by a white band dorsally. Cheeks often plain brown, with a faint blotch only vaguely visible. A broad brown band extending from anterior lower margin of orbit to lower margin of upper lip. Another, less intense band often reaching from the posterior lower margin of orbit to posterior end of maxilla; if present, it is darkest near the maxilla, and is sometimes Y-shaped. Males often with 3–5 vertical streaks anteriorly on the head, which extend onto the upper lip. The medium streak is split between the eyes, then joins again, extending close to the posterior margin of the orbit. Upper sides of head with diffuse, confluent spots, or plain medium brown. Posterior lower cheeks, operculum and occasionally pectoral fin base with diffuse, dark brown spots of varying size, some as large as the pupil. Lower sides of head light brown, chin usually dark brown, followed by a dark brown band which ascends posteriorly from the lower margin of the lower lip slightly anterior of the corner of the mouth, joining with the band of the other side and forming an angular mark. Another, parallel band crossing the branchiostegal rays, but not joining the band of the other side.

Upper sides of body with a pattern of dark brown or blackish brown blotches, reaching across the upper two-thirds of the body to below the lateral line, in six groups of blotches forming three longitudinal rows, except for a single, elongate blotch on the posterior caudal peduncle. The blotches in the upper longitudinal row are usually most pronounced, extending on the dorsal fin base or forming saddles with the blotches on the other side of the body. The blotches of the second row are often forming characteristic groups with those of the upper row, while the blotches of the third row are situated further posteriorly. The blotches are usually equal in size; occasionally, two blotches may join to form a single, elongate blotch.

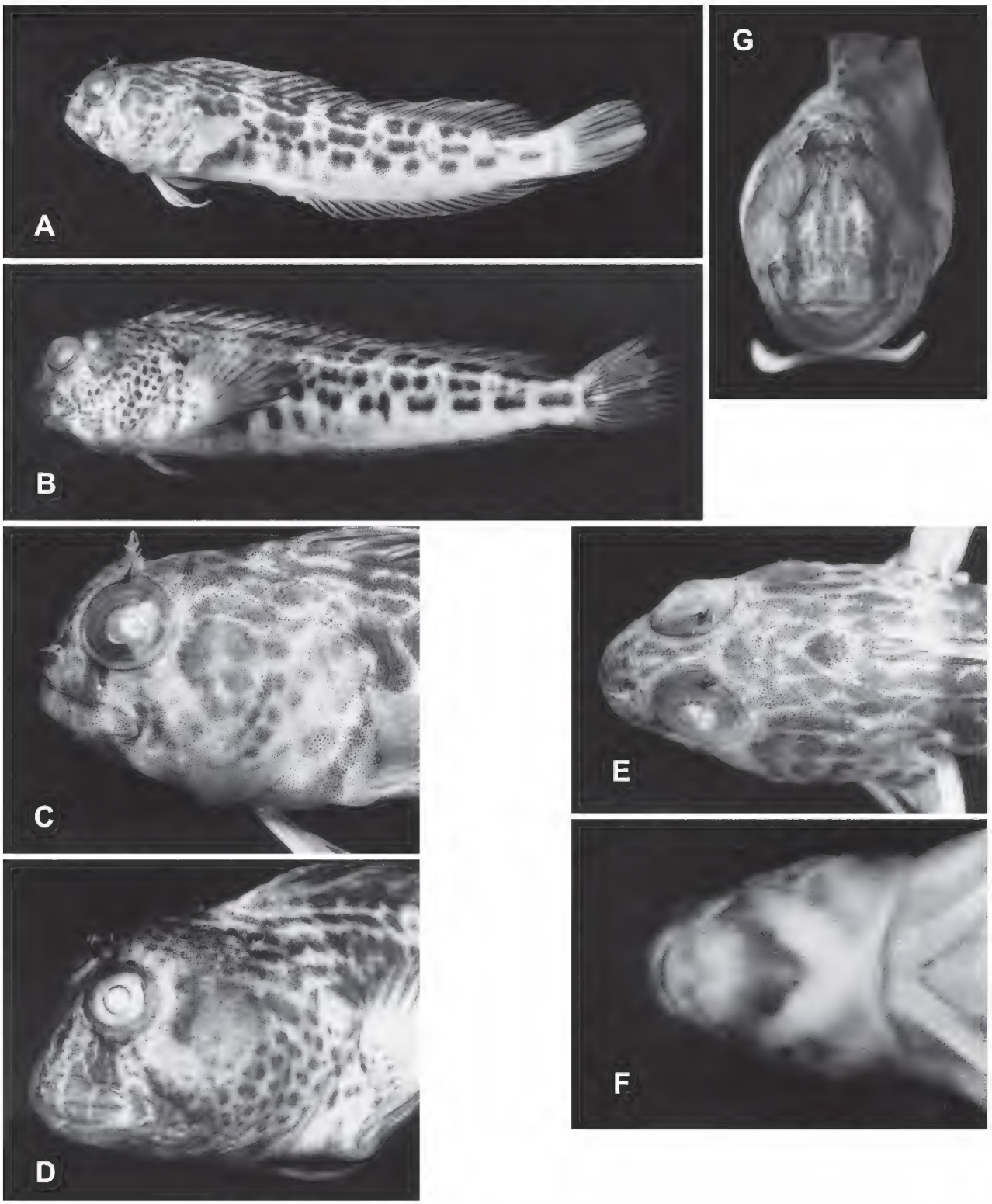

Fig. 4. *Parablennius intermedius* (Ogilby, 1915), Australia. – **A**. AMS I.41874-016, male, 30.5 mm SL, New South Wales, lateral view. **B**. WAM P.27064-011, male, 43.7 mm SL, Queensland, lateral view. **C**. AMS I.41874-016, male, 30.5 mm SL, New South Wales, enlarged lateral view of head. **D**. AMS I.41262-019, male, 52.5 mm SL, New South Wales, enlarged lateral view of head. **E**. AMS I.41874-016, male, 30.5 mm SL, New South Wales, dorsal view of head. **F**. AMS I.41268-015, female, 39.7 mm SL, New South Wales, ventral view of head. **G**. AMS I.41268-015, female, 39.7 mm SL, New South Wales, frontal view of head.

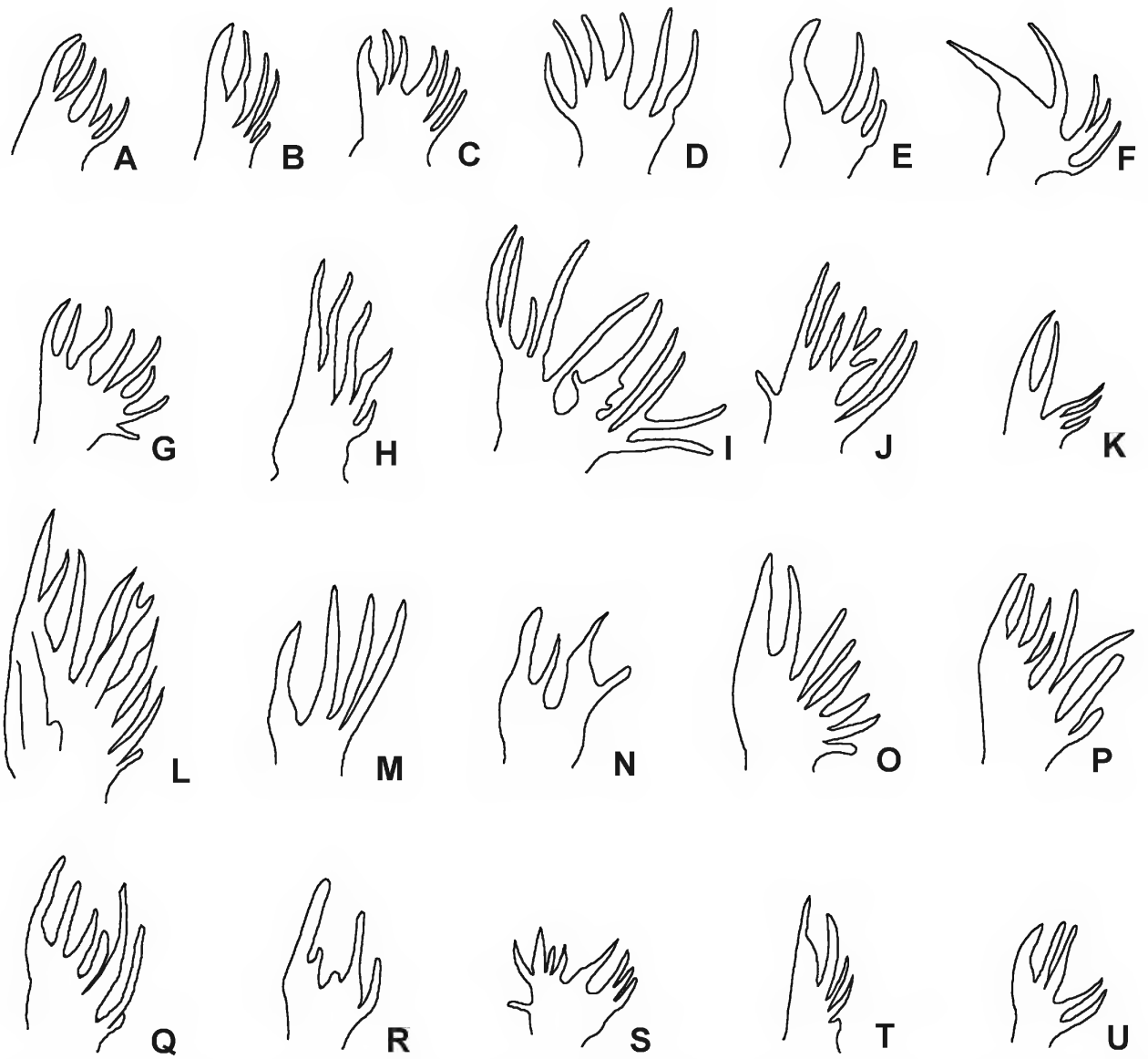

Fig. 5. *Parablennius intermedius* (Ogilby, 1915), Australia, right supraorbital tentacle of males (A–P) and females (Q–U). – **A**. Cape York, Queensland, 40.0 mm SL, 1.4 mm ST. **B**. Cape Ferguson, Queensland, 33.7 mm SL, 1.3 mm ST. **C**. Masthead Island, Queensland, 44.4 mm SL, 1.9 mm ST. **D**. Bagara, Kelly's Beach, Queensland, 43.7 mm SL, 1.7 mm ST. **E–F**. Minnie Waters, New South Wales, 41.4 mm SL, 1.8 mm ST (E), 36.8 mm SL, 2.1 mm TL (F). **G–H**. Seal Rocks, New South Wales, 47.7 mm SL, 2.2 mm ST (G), 51.0 mm SL, 2.8 mm ST (H). **I**. off Balmoral Beach, New South Wales, 64.0 mm SL, 4.5 mm ST. **J**. Bottle and Glass Rocks, New South Wales, 59.9 mm SL, 2.5 mm ST. **K**. Long Reef, Dee Why, New South Wales, 36.5 mm SL, 1.6 mm ST. **L**. Sydney Harbour, Gore Cove, New South Wales, 41.6 mm SL, 2.8 mm TL. **M**. Spooky Point, Angourie, New South Wales, 49.5 mm SL, 2.4 mm ST. **N**. Lennox Head Beach, New South Wales, 50.7 mm SL, 1.4 mm ST. **O–P**. Hastings Point, Cudgera Creek, New South Wales, 42.0 mm SL, 2.3 mm ST (O), 36.2 mm SL, 2.3 mm ST (P). **Q–R**. Hastings Point, Cudgera Creek, New South Wales, 37.7 mm SL, 1.1 mm ST (Q), 37.2 mm SL, 1.2 mm ST (R). **S**. Masthead Island, Queensland, 38.2 mm SL, 1.9 mm ST. **T**. Bagara, Kelly's Beach, Queensland, 28.2 mm SL, 1.5 mm ST. **U**. Cape York, Queensland, 27.6 mm SL, 0.9 mm ST.

The dorsal fin colouration of the male may be variable; that of large adults is usually more pronounced than in smaller specimens. A distal, triangular blotch on the first dorsal fin membrane. Second membrane rarely with a similar blotch. Spinous portion of dorsal fin bordered by a brownish to blackish brown distal band, and one or two bands of brownish spots of variable intensity below. Soft dorsal portion with oblique rows of grey spots. Triangular blotch on first dorsal fin membrane usually missing in female. The female's dorsal fin often only with 2–3 rows of indistinct spots. Median and distal portions of dorsal fin with three slightly oblique rows of brown spots, which

may occasionally join bands; this pattern is most pronounced on the soft portion of the dorsal fin.

Anal fin light yellow to brown with a narrow, dark brown to blackish distal margin. Tips of fin rays whitish. Pectoral and caudal fin rays brownish, membranes white. Pelvic fins whitish, brownish or light grey.

Body colouration usually less pronounced in females than in males. Head streaks and spots on preoperculum and pectoral fin base may be missing or vague in females, but spots on opercle usually present.

Besides the above described most common colour patterns, several variations have been observed. Specimens from Masthead Island/Queensland, Australia are usually missing spots on the head and the opercle. Specimens from Minnie Waters/New South Wales have only 7–9 large blotches on the opercle, each larger than the pupil. Specimens from Port Jackson area may have diffusely spotted lower cheeks, opercle, opercular membranes and pectoral fin base, with the spot diameter slightly less than the pupil; these spots are extending to the body, increasing in diameter posteriorly, almost arranged in longitudinal rows on the posterior body. Another specimen is entirely lacking spots on head and opercle, except a fine, dense spotting on the pectoral fin base. Similar diffuse, dense spots are situated on the anterior and medium thirds of the body, increasing in diameter posteriorly, but not larger than the pupil.

Colour in life (based on a specimen from Shellharbour, New South Wales, photo by S. Schultz, January 2004, published online by The Australian Museum, Sydney, version 15 Oct. 2006, http://www.amonline.net.au/fishes/fishfacts/fish/pintermed3.htm). Head and body ground colouration creamy white, blotches on head orange and brown, stem of supraorbital tentacle orange; eye alternatingly marked with dark red and pink; blotches on sides of body black, bordered with cream, with brown areas in between; dorsal and caudal fins basally cream, distally reddish, with brown and blackish bands and blotches; lower sides of body and lower pectoral fin with silvery bluish spots.

b) New Caledonian populations (Figs. 6–7)

Colour in alcohol. Head and body light to medium brown. Postorbital region in most specimens with a blotch of eye size, situated a little lower than the eye. The lower half of the blotch is a little lighter than the upper half. Postorbital blotch dorsally with a dark-edged border. Postorbital area also with a small, blackish spot. Two parallel dark bands extending from anterior lower margin of orbit to middle of lateral half of upper lip. Another band reaching from the posterior-ventral margin of orbit to posterior end of maxilla. Head anteriorly usually with 3–5 narrow vertical bands consisting of streaks and spots, which extend onto the upper lip. Upper sides of head with dark spots of half pupil size in irregular or longitudinal arrangement. Predorsal area usually with large irregular, black blotch. Opercle and preopercle with irregularly arranged, elongate spots. Lower sides of head light, with a median broad, dark, angular mark and two, slightly narrower dark bands reaching from the corner of the mouth obliquely backwards across the branchiostegal membranes, but rarely joining to an angular mark. Prepectoral area with a broad, vertical, dark band.

Upper half of body with a pattern of dark brown or blackish brown blotches, reaching across the upper two-thirds of the body to below the lateral line, in six groups of blotches forming three longitudinal rows, except for a single, elongate blotch posteriorly on the caudal peduncle; upper longitudinal row consists of six pairs of blotches, which are often interconnected and extend as saddles across the dorsum to the other side of the body. The blotches of the second row often form characteristic groups with those of the upper row, and the blotches of the third row are situated further posteriorly, and extend ventrally as a streak. The blotches are usually equal in size; occasionally, two blotches may join to a single, elongate blotch.

Colouration of the membranes between the unsegmented dorsal fin rays in males with a distal brown band, and an elongate ventral band of dark, oval blotches on the fin rays. Soft dorsal fin distally with a brown streak on the membranes. A distal, triangular blotch on the first interradial dorsal fin membrane of males; blotch is lacking in females; females usually with three oblique, descending rows of spots. Anal fin distally with a dark band in both sexes. Pectoral, pelvic and caudal fins light yellowish brown; the lowermost 3–4 pectoral fin rays and the second and third rays of the pelvic fin slightly darker.

Distribution

This species is known from eastern Australia (Queensland, Cape York area southward; northern and central New South Wales, and Jervis Bay area/Australian Capital Territory), and New Caledonia (southwestern Grande Terre) (Fig. 3); it is found on or adjacent to rocky reefs and in tidal rockpools. Possibly also Solomon Islands (New Georgia); see discussion.

Remarks

The eastern Australian populations of this species were treated as a subspecies of *Parablennius tasmanianus* by Bath & Hutchins (1986). They are now raised to species level as *Parablennius intermedius*. *Parablennius tasmanianus caledoniensis* Bath, 1989 (**n. syn.**) is now found to be a junior synonym of *P. intermedius* (see discussion under 5).

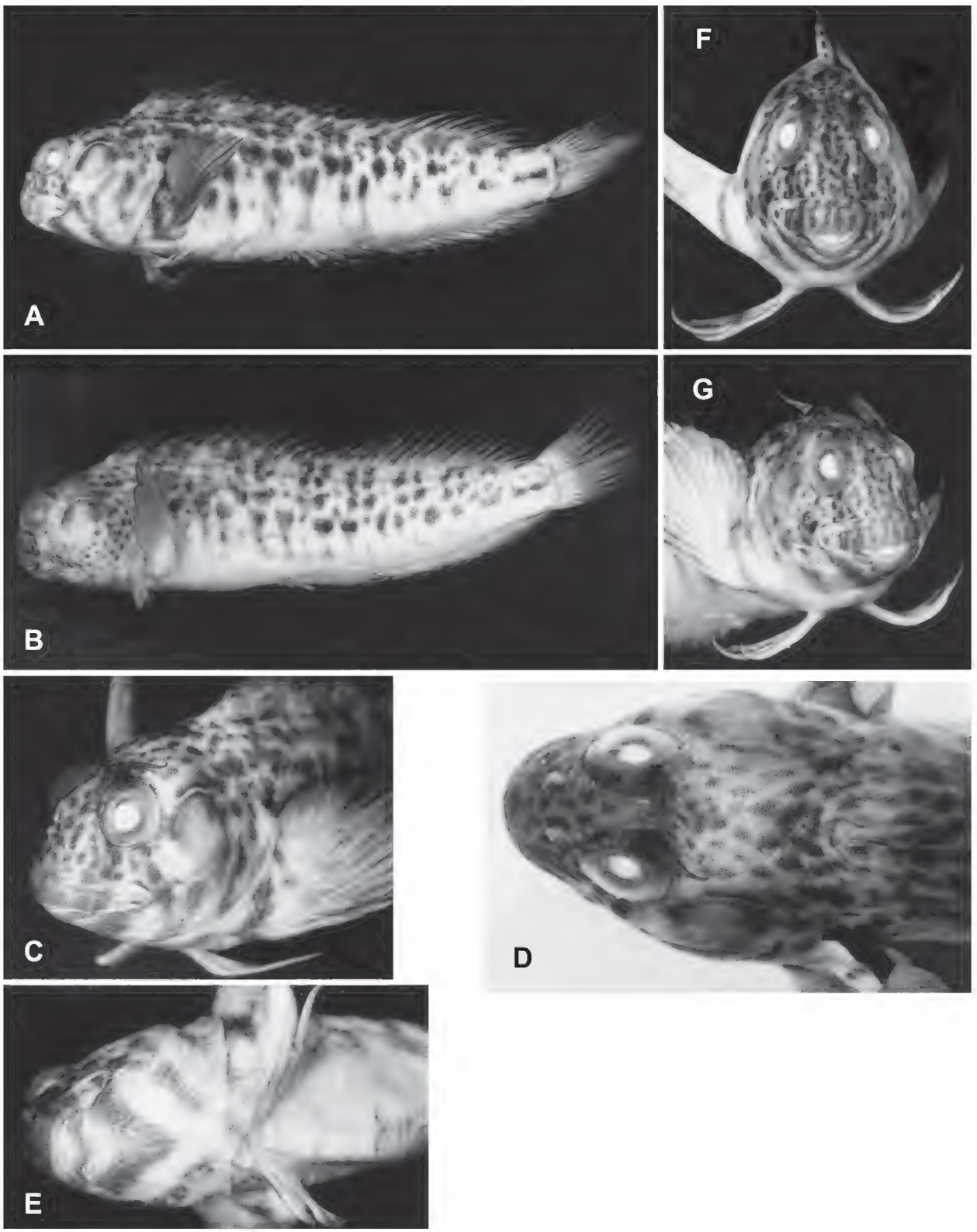

Fig. 6. *Parablennius intermedius* (Ogilby, 1915), New Caledonia. – **A**. SMNS 22624, male, 36.7 mm SL, lateral view. **B**. SMNS 23045, male, 36.2 mm SL, lateral view. **C**. SMNS 22624, male, 36.7 mm SL, enlarged lateral view of head. **D**. SMNS 22624, male, 36.7 mm SL, dorsal view of head. **E**. SMNS 22624, male, 36.7 mm SL, ventral view of head. **F–G**. SMNS 22624, female, 36.2 mm SL, frontal (F) and left frontal (G) views of head.

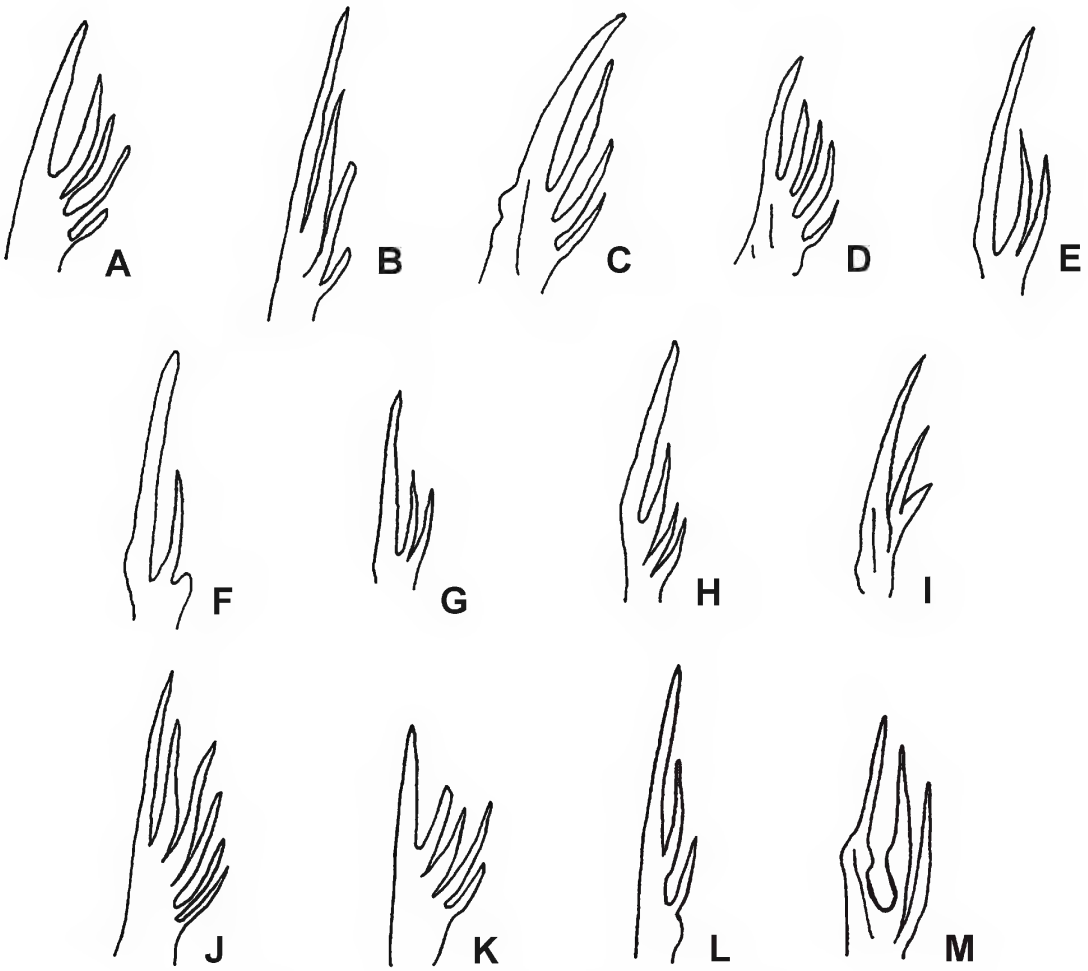

Fig. 7. *Parablennius intermedius* (Ogilby, 1915), New Caledonia, Province Sud, Grande Terre, right supraorbital tentacle of males (A–I) and females (J–M). – **A–B**. Nouméa, Ducos Peninsula, 31.6 mm SL, 1.7 mm TL (A), 36.2 mm SL, 2.0 mm ST (B). **C–D**. Baie de Gouaro, 36.7 mm SL, 2.8 mm ST (C), 34.0 mm SL, 2.0 mm ST (D). **E–H**. Île Nou, 36.2 mm SL, 2.1 mm ST (E), 31.7 mm SL, 2.1 mm ST (F), 31.1 mm SL, 2.1 mm ST (G), 30.7 mm SL, 2.4 mm ST (H). **I**. Nouméa Harbour, 31.6 mm SL, 1.7 mm ST. **J–L**. Nouméa, 33.5 mm SL, 1.7 mm ST (J), 30.6 mm SL, 1.4 mm ST (K), 31.2 mm SL, 2.1 mm ST (L). **M**. Baie de Gouaro, 30.7 mm SL, 1.7 mm ST.

3.3 *Parablennius postoculomaculatus* Bath & Huchins, 1986 (Figs. 8–9)

Parablennius tasmanianus postoculomaculatus Bath & Hutchins, 1986: Bath & Hutchins 1986: 187–192, figs. 24–28, 29a–r (Australia, Houtman Abrolhos, Beacon Island/ Western Australia; holotype: SMF 17092). – Bath 1996: 92 (name in checklist of tribe Parablenniini).

Parablennius postoculomaculatus: Bath 1990: 66 (in key; Western Australia). – Hutchins 1994: 25, 26, 55 (Western Australia, distribution in Leeuwin Province). – Yearsley et al. 1997: Code 37 408068 (Australia; CAAB Code). – Hutchins 2001: 41 (Western Australia; in checklist).

Material

Total: 50 specimens.

Australia, Western Australia: AMS I.19240-001, 1 female, Carnac Island; AMS I.19602-027, 2 males and 2 females, Geographe Bay, 33°20'S 115°34'E, 21 Oct. 1972; SB uncat., 1 male and 1 female, paratypes of *Parablennius tasmanianus postoculomaculatus* Bath & Hutchins, same data as the holotype; SMF 17092, holotype of *Parablennius tasmanianus postoculomaculatus* Bath & Hutchins, male, Houtman Abrolhos, Beacon Island, 31 Aug. 1977; SMF 17093–17094, 1 male and 1 female, paratypes of *Parablennius tasmanianus postoculomaculatus* Bath & Hutchins, same data as the holotype; SMNS 14892, 1 female, Torbay, Cosy Corner, 26 km west of Albany, 33°55'36"S 122°35'07"E, R. Fricke, 10 Oct. 1992; SMNS 14898, 4 females, Peaceful Bay, 20 km southeast of Walpole, 35°02'49"S 116°50'46"E, 0–0.8 m depth, R. Fricke, 11 Oct. 1992; SMNS 14918, 6 males, 2 females and 1 juvenile, Rottnest Island, Parker Point, southeastern side of island, 35 km west of Perth, 32°01'36"S 115°31'40"E, R. Fricke, 19 Oct. 1992; WAM P.25833-002, 2 males, South Muiron Island, 21°45'S 114°10'E, 15 June 1977; WAM P.25850-008, 7 males and 3 females, paratypes of *Para-*

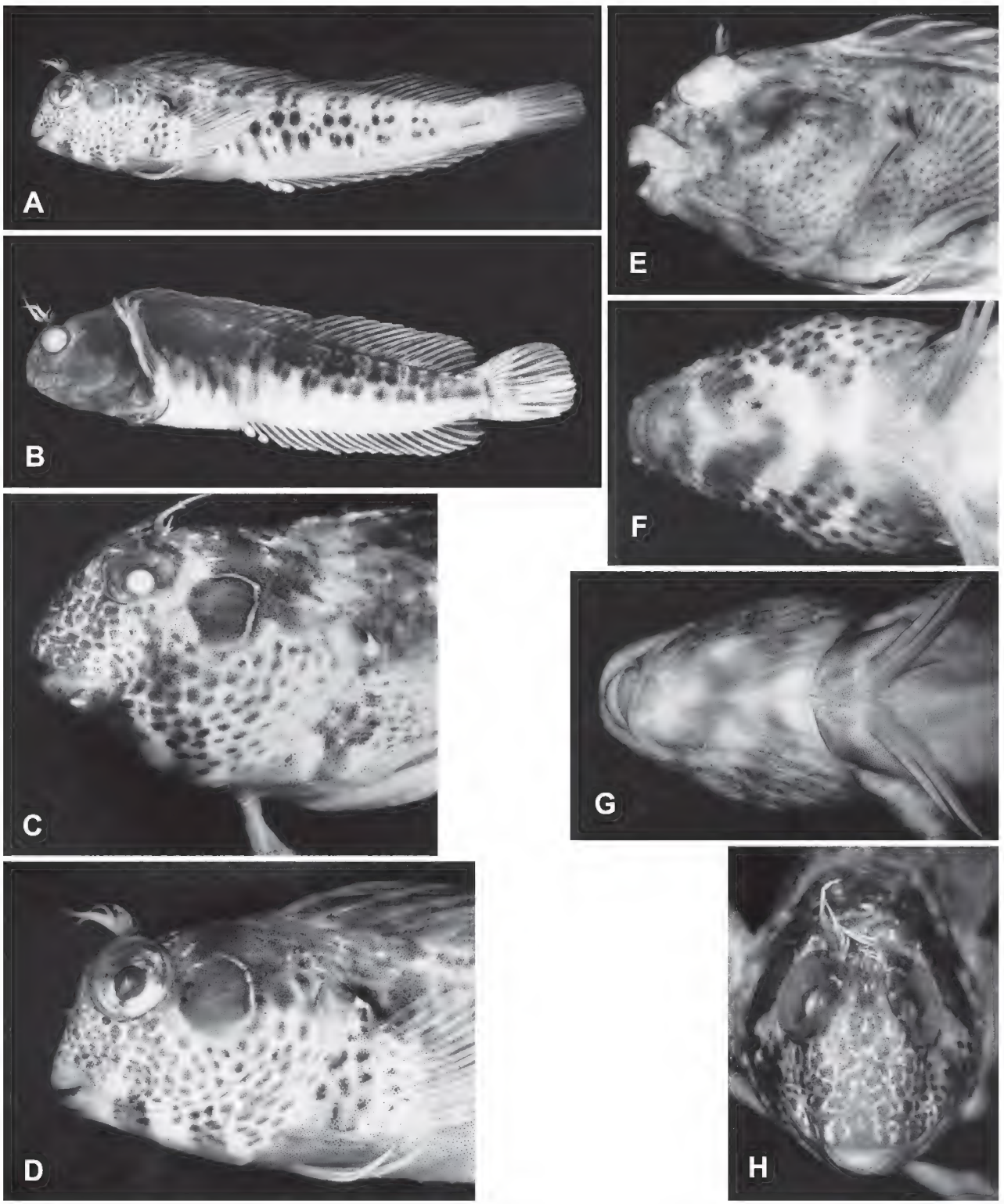

Fig. 8. *Parablennius postoculomaculatus* Bath & Hutchins, 1986, Western Australia. – **A**. SMF 17092, male, 40.7 mm SL, holotype, lateral view. **B**. WAM P.27968-009, male, 44.3 mm SL, lateral view. **C**. SMNS 14918, male, 40.8 mm SL, enlarged lateral view of head. **D**. SMF 17092, male, 40.7 mm SL, holotype, enlarged lateral view of head. **E**. SMNS 14898, female, 66.3 mm SL, enlarged lateral view of head. **F**. SMNS 14918, male, 40.8 mm SL, ventral view of head. **G**. SMNS 14898, female, 66.3 mm SL, ventral view of head. **H**. SMNS 14918, male, 40.8 mm SL, frontal view of head.

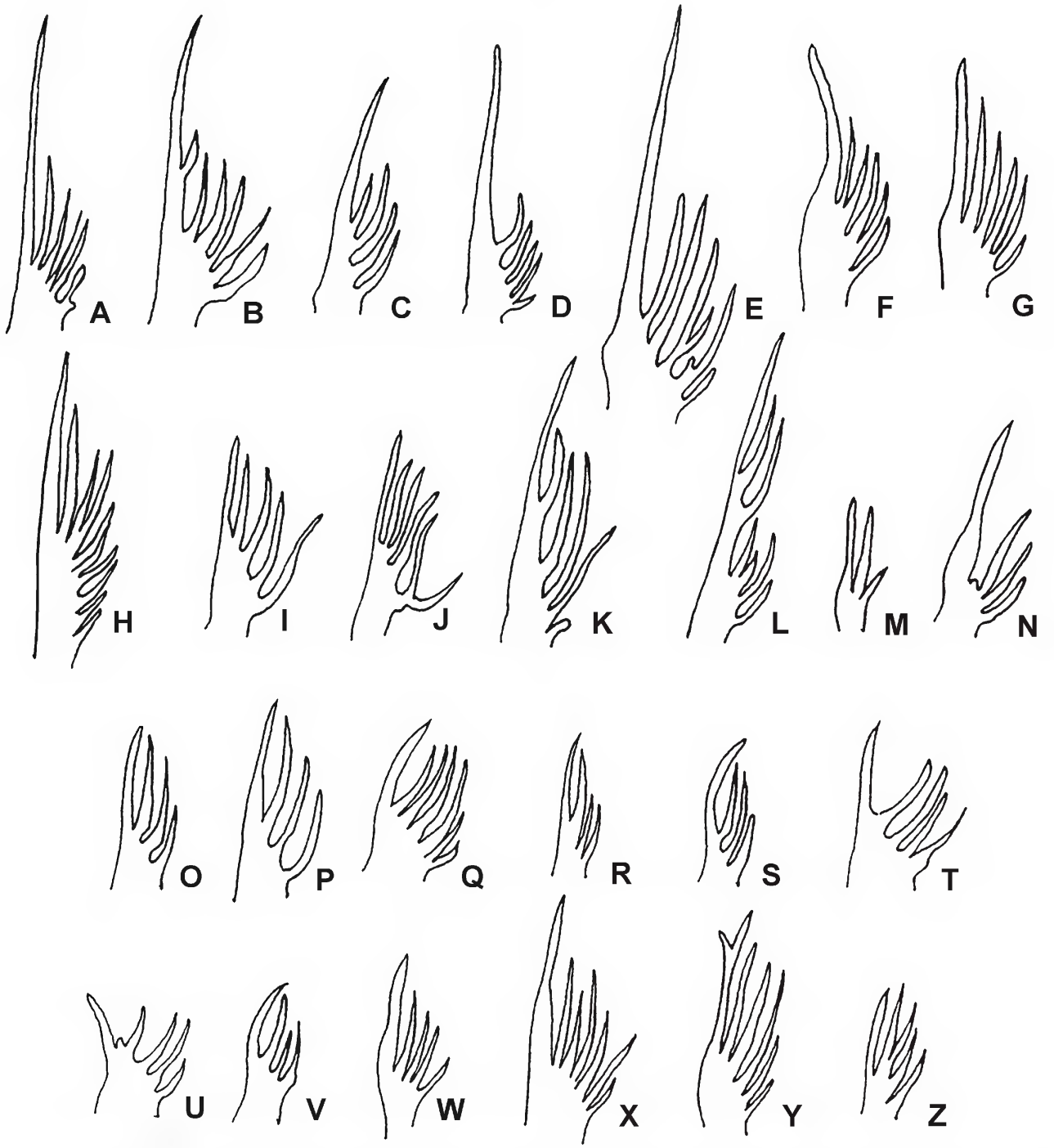

Fig. 9. *Parablennius postoculomaculatus* Bath & Hutchins, 1986, Western Australia, right supraorbital tentacle of males (A–N) and females (O–Z). – **A**. South Muiron Island, 31.5 mm SL, 3.2 mm ST. **B–C**. Point Quobba, 44.3 mm SL, 4.5 mm ST (B), 34.6 mm SL, 2.1 mm ST (C). **D–E**. Beacon Island, Houtman Abrolhos, 39.8 mm SL, 5.3 mm ST (D), 45.0 mm SL, 7.4 mm ST (E). **F–H**. Parke Point, Rottnest Island, 40.8 mm SL, 2.4 mm ST (F), 43.5 mm SL, 2.3 mm ST (G), 65.3 mm SL, 6.2 mm ST (H). **I–J**. Geographe Bay, 48.1 mm SL, 3.3 mm ST (I), 40.6 mm SL, 3.5 mm ST (J). **K–L**. Quarry Bay, 64.5 mm SL, 4.0 mm ST (K), 41.4 mm SL, 6.3 mm ST (L). **M**. Cosy Corner, Torbay, 30.3 mm SL, 1.4 mm ST. **N**. Two Peoples Bay, 37.8 mm SL, 2.8 mm ST. **O**. Point Quobba, 33.5 mm SL, 1.5 mm ST. **P–R**. Beacon Island, Houtman Abrolhos, 46.6 mm SL, 2.2 mm ST (P), 45.4 mm SL, 1.9 mm ST (Q), 38.4 mm SL, 2.0 mm ST (R). **S**. Carnac Island, 42.0 mm SL, 1.9 mm ST. **T–U**. Geographe Bay, 62.0 mm SL, 2.4 mm ST (T), 47.8 mm SL, 1.3 mm ST (U). **V**. Bunkers Bay, 41.5 mm SL, 1.8 mm ST. **W–Z**. Peaceful Bay, 64.3 mm SL, 3.7 mm ST (W), 66.3 mm SL, 4.8 mm ST (X), 48.5 mm SL, 3.6 mm ST (Y), 74.5 mm SL, 3.0 mm ST (Z).

blennius tasmanianus postoculomaculatus Bath & Hutchins, same data as the holotype; WAM P.26545-008, 3 males, Quarry Bay, Augusta, 34°19'S 115°09'E, 2 Feb. 1979; WAM P.2601-004, 2 males, Two Peoples Bay, 13 Apr. 1980; WAM P.27880-011, 1 female, Bunkers Bay, 8 Dec. 1982; WAM P.27949-018, 1 female juvenile, Jurien Bay, 30°08'S 115°00'E, 9 Apr. 1983; WAM P.27967-031, 3 males and 1 female, Point Quobba, Fitzroy Reefs, 25 Apr. 1983; WAM P.27968-009, 2 males and 1 female, 2 km north of Point Quobba, 25 Apr. 1983.

Diagnosis

A species of *Parablennius* with 16 (rarely 15 or 17) segmented dorsal fin rays and 18 (rarely 16–17) segmented anal fin rays; supraorbital tentacle in both sexes consisting of a long, stout main tentacle, with three to (rarely) nine side branches; with 120–266 pores of the head lateral line system (mean 207.4); postorbital region with a round to oval, light brown blotch, bordered by a usually segmented white, dark-edged streak; lower half of cheek, sides of the upper lip, suborbital area, branchiostegal membranes, pectoral fin base and basal one-third of pectoral fin with numerous medium to blackish brown blotches; elongate rows of dark blotches in 6–7 groups along the upper two-thirds of the body.

Colour description

Colour in alcohol. Head and body light brown to brown. Postorbital region with a light brown round or slightly oval blotch, situated a little lower than the eye, bordered by a usually segmented white, dark-edged streak. Lower half of cheek, sides of the upper lip, suborbital area, branchiostegal membranes, pectoral fin base and basal one-third of pectoral fin with numerous medium to blackish brown blotches; this pattern of blotches may extend ventrally to the lateral margin of the angular mark on the lower side of the head, and to the ventral base of the branchiostegal rays. Part of tip of chin brownish. Lower sides of head with a light to dark brown band, extending from the corner of the mouth obliquely down, in males joining the band of the other side to form an angular mark, which is lighter in the midline than laterally. Another parallel streak behind reaching from the antero-ventral margin of the opercle to the anterior corner of the opercular membrane, not connected with the streak of the other side of the head.

Median one-third of body with concise, upper one-third with vague brown blotches, arranged in 6–7 groups along the sides of the body. The upper row connected with the blotches of the other side of the body forming faint saddles, barely reaching the basal part of the dorsal fin, in more irregular arrangement than the blotches below. The blotches in the median and lower rows are mostly round to oval. Caudal peduncle occasionally with a slightly larger, dark blotch. Lower sides of body at the anal fin base in some specimens with 6–7 light grey blotches. Some specimens may have additional small silvery white spots on the upper one-third of the body, and larger such spots on the lower two-thirds. Body colouration less intensive in females and adult males.

Dorsal, anal and pectoral fins in males light grey, in females whitish or yellowish white. First interradial membrane of the unsegmented dorsal fin in males with a small, triangular, faintly dusky blotch. Remaining parts of the dorsal fin either with diffuse melanophores which are more densely set distally, or with brownish or blackish blotches in oblique rows.

Colour in life. Head and body greenish grey or light orange. Colour pattern similar to colour in alcohol as described above, but with a few bright red spots in between. Dorsal, anal and caudal fins greenish yellow to orange.

Distribution

This species is endemic to Western Australia, occurring from South Muiron Island south to Albany area (Fig. 3); it lives in shallow water on or adjacent to rocky reefs or in tidal rockpools.

Remarks

The species was originally described as a subspecies of *Parablennius tasmanianus*. It is now raised to species level (see discussion under 5).

4 Key to Australian and New Caledonian species of *Parablennius* (excluding Norfolk Island)

1 Segmented dorsal fin rays 15–17. . . . . **2**
– Segmented dorsal fin rays 18–19. – Southern New South Wales west to Southern Australia, south to Tasmania. . . . . ***P. tasmanianus***
2 Head lateral line pores 120–266, mean 207.4. Males with intense spotting on lower side of head. – Western Australia. . . . . ***P. postoculomaculatus***
– Head lateral line pores 92–190, mean 144.1 (eastern Australian populations) or 126.6 (New Caledonian populations). Males without spotting or with few spots on lower side of head. . . . . ***P. intermedius***

5 Discussion

The additional, fresh material previously classified as *Parablennius tasmanianus intermedius* from eastern Australia and *Parablennius tasmanianus caledoniensis* from New Caledonia enabled the author to review the identity of the populations. The main characters distinguishing the species of this complex are the numbers of fin rays, the shape of the supraorbital tentacle, the head lateral line system, and the head and body colouration.

Australian and New Caledonian *Parablennius* species show a high variability in many characters. Especially the

supraorbital tentacle cannot be considered a good character to distinguish species, as it is much too variable (Figs. 2, 5, 7, 9), though eastern Australian populations now classified as *P. intermedius* tend to have a hand-shaped tentacle (Fig. 5), while other species/populations have a more slender tentacle. *Parablennius tasmanianus* has a long and stout main tentacle with a relatively narrow base (Fig. 2) and several lateral branches which may be divided, increasing in number with body length; males have 4–30 branches, females 5–9. The supraorbital tentacle of *P. postoculomaculatus* is similar to *P. tasmanianus*, but with a lateral tentacle which is often as long as the main tentacle, especially in females. In males, the lateral tentacle has 2–14 side branches; 3–4 (–7) in females.

In *Parablennius intermedius*, the supraorbital tentacle is highly variable. The eastern Australian populations have usually a broad base; the main tentacle is often not longer than the side branches, which usually grow out of the base, and may be of equal length. Some side branches may be divided. Males usually possess more numerous side branches than females. Specimens of the New Caledonian populations usually have a long main tentacle; the branches either originate from the main tentacle or from the base. The 13 examined specimens had 2–6 side branches.

The number of branched rays in the dorsal fin is (16–)18–19 in *Parablennius tasmanianus*, (15–)16–17(–18) in *P. intermedius* and (15–)16(–17) in *P. postoculomaculatus*. *Parablennius tasmanianus* has (18–)19–20 branched anal fin rays, *P. intermedius* (17–)18–19, and *P. postoculomaculatus* (16–)18 (Tab. 1).

The pores in the head lateral line system are compared in Tab. 2. Eastern Australian populations of *P. intermedius* have 92–190 pores (mean 144.1), New Caledonian populations 108–139 (mean 126.6). However, as the specimens examined from eastern Australia had 20.3–65.2 mm SL (mean 39.7), but the New Caledonian specimens were much smaller, 30.6–35.7 mm SL (mean 33.3), and the number of head lateral line pores increases with body length, the difference in the mean pore number between the two population groups is not considered to be of taxonomical relevance. However, there is a significant difference between the mean head lateral line pore numbers of *P. intermedius* and the other species in the complex. *Parablennius tasmanianus* has a mean of 178.4, and *P. postoculomaculatus* 207.4.

The head and body colouration is redescribed above from fresh specimens preserved in ethanol. The three species are relatively variably coloured regarding age, sex, and geography. Most specimens of *P. tasmanianus* have a vague brown blotch behind the eye, bordered by a light streak above and a dark streak anteriorly. The sides of the head often bear two oblique dark bands; the lower side of head usually has no angular dark mark (which is incomplete if at all present). Cheeks, opercle, pectoral fin base of side of body rarely with spots, and if present, only in single individuals.

Parablennius intermedius likewise has a dark blotch behind the eye that is bordered with black anteriorly and posteriorly, occasionally also with white dorsally. This species typically has a pattern of streaks and blotches on the head. The frontal side usually bears five narrow vertical streaks, with two additional irregular lateral bands. The dorsal side of head with 4–5 rows of spots or short bands. The lower side of the head has a narrow angular mark, with a second, broader, interrupted mark behind. Cheeks with diffuse dark spots, which are usually more pronounced in eastern Australian specimens than in New Caledonian specimens.

Typical specimens of *Parablennius postoculomaculatus* have an eye-sized, round to oval, brownish ocellus behind the eye. The cheeks and sides of head bear numerous brown blotches; it is unique for this species that they are reaching to the lower side of the head and to the ventral base of the branchiostegal rays. Lower side of head with an angular dark mark, and another, interrupted mark behind.

The most reliable characters to distinguish species in this complex include dorsal fin rays, mean number of head

Tab. 1. Dorsal and anal fin rays of Australian and New Caledonian species of *Parablennius*.

Species	Area	Dorsal fin									Anal fin				
		XII, 15	XII, 16	XIII, 16	XI, 17	XII, 17	XI, 18	XII, 18	XIII, 18	XII, 19	II, 16	II, 17	II, 18	II, 19	II, 20
P. intermedius	New South Wales and Queensland/Australia	1	39	1	1	47	–	1	–	–	–	4	67	19	–
	New Caledonia/France	–	6	1	–	6	–	–	–	–	–	2	7	4	–
P. postoculomaculatus	Western Australia	2	25	–	–	4	–	–	–	–	1	1	29	–	–
P. tasmanianus	New South Wales/Australia	–	4	–	–	23	–	5	–	–	–	–	9	20	3
	Victoria/Australia	–	–	–	–	2	–	21	1	5	–	–	1	5	23
	South Australia	–	–	–	–	1	–	5	–	3	–	–	–	4	5
	King Island and Flinders Island/Australia	–	–	–	–	2	1	7	–	2	–	–	–	2	10
	Tasmania/Australia	–	1	–	–	1	–	10	–	6	–	–	–	4	14

Tab. 2. Head lateral line pores of Australian and New Caledonian species of *Parablennius*.

Species, Area	Number of specimens	SL	Mean SL	Head lateral line pores	Mean head lateral line pores
P. intermedius, New South Wales and Queensland/Australia	61	20.3–65.2	39.7	92–190	144.1
P. intermedius, New Caledonia/France	11	30.6–36.7	33.3	108–139	126.6
P. intermedius, combined	72	20.3–65.2	38.7	92–190	141.4
P. postoculomaculatus, Western Australia	18	30.3–74.5	48.8	120–266	207.4
P. tasmanianus, New South Wales and South Australia to Tasmania/Australia	22	25.0–86.4	50.4	102–304	178.4

lateral line pores, and the head colouration. Using the characters described above, it is concluded that *Parablennius tasmanianus*, *P. intermedius* and *P. postoculomaculatus* are sufficiently distinguished to be raised to species level. The population previously classified as *P. tasmanianus caledoniensis*, which has a smaller adult size than other populations in the complex, was found to perfectly agree in its fresh colour pattern with eastern Australian *Parablennius intermedius*. The mean number of head lateral line pores is even a little lower than in eastern Australian populations, but agrees with the number in small specimens of *P. intermedius*. It is therefore concluded that *Parablennius tasmanianus caledoniensis* is a junior synonym of *P. intermedius*.

The identification of specimens in the Australian/New Caledonian *Parablennius* complex is not easy. Usually, a series of 10–20 specimens is needed to know the mean number of head lateral line pores. A single specimen of *Parablennius* from the Solomon Islands is known to the author, but could not yet be identified to the species level; it is, however, assumed that *Parablennius intermedius* may range east to the Solomon Islands.

Specimens of the species of *Parablennius* are known to occur on rocky substrates, usually preferring hard rock including plutonic rocks, volcanic rocks and metamorphic rocks, but rarely living on sediment rock and never found on coralline rock. Such hard rock substrates are uncommon in many areas of the Southwest Pacific tropics. In Grande Terre/New Caledonia, for example, there is very little metamorphic rock habitat in the littoral area, but coralline rocks or fringing reefs are much more common, and much more frequently sampled for fish specimens. Furthermore, as *Parablennius* is most common in and probably adapted to water temperatures of warm temperate habitats, it relies on cool upwelling conditions if it occurs in the tropics. Such rock habitats in upwelling areas are rarely sampled thoroughly. A higher sampling effort in such habitats would probably provide additional material of *Parablennius* to clarify the range of the species into the tropical Southwest Pacific.

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Manuscript received: 5.IV.2007, accepted: 21.V.2007.

Amphibians in the border region between Uruguay and Brazil: Updated species list with comments on taxonomy and natural history (Part I: Bufonidae)[1]

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Abstract

The border region between Uruguay and the Brazilian state of Rio Grande do Sul comprises four major biomes, i. e. the coastal dune zone, adjacent wetlands, low hill ranges (cuchillas), and grassland (pampas). All these environments provide different microhabitats for amphibians, such as continental lagoons, rivers, small streams, ponds and temporary water bodies. This habitat diversity is reflected by high species diversity, but the amphibian fauna in this region is yet poorly studied. Recent fieldwork revealed several new records for anurans, including a recently described species of toad, *Chaunus achavali*. In our publication we provide an updated check list of the species belonging to the family Bufonidae (toads) occurring in this region, including taxonomical comments, conservation issues, natural history notes, zoogeographical considerations and an updated bibliography. A total amount of 13 species of Bufonidae is known from the study area belonging to the genera *Chaunus* (formerly *Bufo*) and *Melanophryniscus*. *Chaunus* is represented by seven species in three taxonomic groups (*C. marinus*, *C. granulosus* and *C. crucifer* groups), whereas *Melanophryniscus* is represented by six species in three groups (*M. stelzneri*, *M. moreirae* and *M. tumifrons* groups). We present a key for the identification of these bufonid species in the study region. Based on geographical distribution patterns of the species involved, we distinguish five main ecological groups: coastal species inhabiting sandy soil layers (*Chaunus arenarum* and *Melanophryniscus montevidensis*); species shared with the Argentinean mesopotamic region (*Chaunus granulosus* group); species characteristic for the chacoan region (*Chaunus schneideri*); species associated with the low hill regions of Uruguay and southern Rio Grande do Sul (most taxa belonging to *Melanophryniscus*); two species of *Chaunus* (*C. ictericus*, *C. henseli*) are associated with the Atlantic forest biome further to the north being untypical for the border region.

Keywords: Anura, Bufonidae, *Bufo*, *Chaunus, Melanophryniscus*, checklist, nomenclature, zoogeography, conservation, Uruguay, Brazil.

Zusammenfassung

Die Grenzregion zwischen Uruguay und dem brasilianischen Bundesstaat Rio Grande do Sul umfasst vier große Naturräume, nämlich die Dünenzone an der Küste, die angrenzenden Feuchtgebiete, die Region der Hügelketten (Cuchillas) und das Grasland (Pampas). All diese Lebensräume beinhalten unterschiedliche Mikrohabitate für Amphibien, beispielsweise Süßwasserlagunen, Flüsse, Bäche, Teiche und temporäre Wasseransammlungen. Diese Habitatvielfalt spiegelt sich in einer hohen Anurendiversität wider. Neuere Feldforschungen erbrachten mehrere Erstnachweise für Froschlurche, einschließlich einer neuen Krötenart, *Chaunus achavali*. In der vorliegenden Arbeit stellen wir eine aktualisierte Checkliste zusammen, die alle in dieser Grenzregion vorkommenden Arten der Echten Kröten (Familie Bufonidae) umfasst, einschließlich taxonomischer Kommentare, Angaben zum Schutz und zur Lebensgeschichte, zoogeographischer Betrachtungen und einer aktualisierten Bibliographie. Insgesamt sind aus dem Studiengebiet 13 Arten Bufonidae bekannt, die zu den Gattungen *Chaunus* (bisher *Bufo*) und *Melanophryniscus* zählen. *Chaunus* ist mit sieben Arten in drei taxomomischen Gruppen vertreten (*C. marinus*-, *C. granulosus*- und *C. crucifer*-Gruppe), *Melanophryniscus* mit sechs Arten in drei Gruppen (*M. stelzneri*-, *M. moreirae*- und *M. tumifrons*-Gruppe). Wir präsentieren einen Schlüssel zur Bestimmung der Krötenarten in der untersuchten Region. Auf Basis der geographischen Verbreitungsmuster der Arten sind fünf ökologische Großgruppen zu unterscheiden: Arten der Küstenregion, die sandige Böden bewohnen (*Chaunus arenarum* und *Melanophryniscus montevidensis*); Arten der mesopotamischen Region Argentiniens (*Chaunus granulosus*-Gruppe); Arten der Chaco-Region (*Chaunus schneideri*); Arten, die assoziiert sind mit der Hügelregion Uruguays und des südlichen Rio Grande do Sul (die meisten *Melanophryniscus*-Taxa). Zwei *Chaunus*-Arten (*C. ictericus*, *C. henseli*) sind charakteristisch für den Atlantischen Regenwald weiter im Norden und erreichen das Untersuchungsgebiet nur ganz am Rande.

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[1] This contribution is dedicated to our colleague Marcos Di-Bernardo (1963–2006) who died of cancer all too fast, and will be missed by the many friends who were privileged to work with him.

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1 Introduction

The amphibian fauna in the border region between Uruguay and the Brazilian state of Rio Grande do Sul has received little attention yet in the history of field surveys in both states, and there is only sparse information on the species richness and life history of anurans in this poorly studied region. Occasional field studies in the last decade provided new records for species previously unknown for this area, i. e. *Dendropsophus minutus* (Olmos et al. 1997), *Scinax fuscovarius* (Arrieta & Maneyro 1999), *Leptodactylus furnarius* (Canavero et al. 2001), *Melanophryniscus sanmartini* (Naya & Maneyro 2001), *Hypsiboas albopunctatus* (Kwet et al. 2002), *Melanophryniscus pachyrhynus* (Borteiro et al. 2005), and *Physalaemus cuvieri* (Maneyro & Beheregaray in press). Additionally, a new toad species, *Chaunus achavali* (Maneyro et al. 2004), was recently described based upon specimens collected in this region.

Although there are some field guides and general checklists for Uruguayan anurans (Klappenbach & Langone 1992; Langone 1995; Achaval & Olmos 2003, Núñez et al. 2004) comprising also the border region between Uruguay and Brazil, only a single specific checklist for this region was published so far (Braun & Braun 1974). Based on collections in the Uruguayan departments Artigas, Rivera and Cerro Largo, Braun & Braun (1974) cited 21 amphibian species, but the fauna from neighbouring areas in Rio Grande do Sul was not considered in this publication. The only available information comprising localities in Rio Grande do Sul is found in Braun (1978), who published an inventory of poisonous species of Bufonidae, and in the summarised data in the checklist of the amphibians of Rio Grande do Sul of Braun & Braun (1980).

Besides these general contributions, there are only two articles published before 1997 providing relevant information about amphibians of the northwestern border region, i. e. Kehr (1983) and Lema & Braun (1993). The study of Kehr (1983) refers to two hylids, *Lysapsus limellus* (for the first time cited from Brazil, based on specimens from Quarai) and *Scinax berthae* (recorded from Santana do Livramento). The publication of Lema & Braun (1993) lists specimens collected by the naturalist William Wright Milstead and includes two localities in our study area, Uruguaiana (a record of *Leptodactylus latinasus*) and Dom Pedrito (a record of *Hypsiboas pulchellus*). Regarding the southeastern part of our study region, there are two older inventories of amphibian species, i. e. one for the Taim reserve in Brazil (Gayer et al. 1988) and another for the Rocha department in Uruguay (Maneyro et al. 1995). Increasing field activities in the last decade yielded in additional publications by various authors, i. e. two book chapters on the amphibians in the Candiota region of Rio Grande do Sul (Di-Bernardo & Kwet 2002; Di-Bernardo et al. 2004) and a study on reproduction of *Pseudis minutus* (Melchiors et al. 2004). Finally, a checklist of the herpetofauna at Cabo Polonio, Rocha department, was recently published by López (2006). However, a summarizing view and actualisation of these specific data is urgently needed, not only for biologists but also as a relevant tool for local conservationists and political decision-makers.

Many threats have been reported from this border area, which might affect amphibian populations. Rice crops in the north (Artigas department) and southeast (mainly Rocha, Treinta y Tres and Cerro Largo departments) of Uruguay (Ministerio de Ganadería, Agricultura y Pesca 2000) and on the South Brazilian coast (Da Motta Marques et al. 2002) produce dramatic changes in the natural drainage dynamics. The unchecked use of Roundup and other pesticides, which are assumed to play an important role in the global amphibian decline (e. g. Relyea 2005), might have negative effects on the local herpetofauna. Additionally tourism and leisure activities in this region, mainly on the oceanic shores, generate water pollution and favor urbanisation among other impacts, which affect amphibian populations as reported by Langone (1995) and Maneyro & Langone (2001). In northern and northwestern Uruguay, the forestation with introduced *Pinus* and *Eucalyptus* was recently developed (mainly in Rivera and Tacuarembó departments); this agricultural activity generates habitat fragmentation and has direct impact on local amphibian populations, e. g. by the destruction of breeding sites after harvesting (Dupuis et al. 1995; Knutson et al. 1999). Bencke (2003) addressed conservation issues in Rio Grande do Sul; especially in the Candiota region, air pollution and contamination of rivers and standing water bodies, due to combustion of coal in power houses, should have negative effects on amphibians (Di-Bernardo & Kwet 2002; Di-Bernardo et al. 2004).

The aim of our publication is, to review the available data for this poorly known and perhaps threatened amphibian fauna in the border region between Uruguay and Brazil, and to provide an actualised checklist, including a list of synomyms, comments on natural history and bibli-

ography. This publication on the family Bufonidae is the first contribution in a threepart series comprising all amphibian species in this area.

Acronyms of depositories

MCN Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre, Brazil)
MCT Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Brazil)
MNHN Museo Nacional de Historia Natural y Antropología (Montevideo, Uruguay)
MNHNP Muséum National d'Histoire Naturelle (Paris, France)
NHMB Naturhistorisches Museum (Basel, Switzerland)
RMNH Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)
UFRGS Universidade Federal do Rio Grande do Sul (Porto Alegre, Brazil)
SMNS Staatliches Museum für Naturkunde (Stuttgart, Germany)
ZMB Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)
ZMUC Universitets København, Zoologisk Museum (Copenhagen, Denmark)
ZUFSM Universidade Federal de Santa Maria (Brazil)
ZVCB Colección de Zoología Vertebrados, Facultad de Ciencias (Montevideo, Uruguay)

Acknowledgements

We are grateful to Mariana Beheregaray, Mónica Brandimarti, Andrés Canavero, Arley Camargo, Inés da Rosa, Rafael de Sá, Marcos Di-Bernardo, Natan Maciel, Dietrich Mebs, Janaine Melchiors, Tatiana Miranda, Daniel Naya, Diego Núñez, Andreas Schlüter and Mirco Solé for valuable help during our field studies. We also thank COFUSA [Compañía Forestal Uruguaya Sociedad Anónima] and Wolf Engels for economical and logistical support during the fieldwork and Frank Glaw and Andreas Schlüter for comments on the manuscript. The following persons allowed us to work in the scientific collections under their care: Sonia Cechin (ZUFSM), José A. Langone (MNHN), Marcos Di-Bernardo (MCT), Marcio B. Martins (MCN) and Laura Verrastro (UFRGS). Fabiola Rezende (MCN), Glaucia Funk Pontes (MCT) and Luis Fernando Marin (UFRGS) provided their help during our work in the collections. Frederico Kolenc, Diego Baldo, Daniel Bühler and Marcelo Casacuberta provided fotos. The first author of the present paper has a doctoral fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) at the Pontifícia Universidade Católica do Rio Grande do Sul.

2 Material and methods

2.1 Study area

The study region is defined by the borderline between the Brazilian state of Rio Grande do Sul and Uruguay ranging from Cuareim River in the northwest to Barra do Chui in the southeast (Fig. 1). Data were collected from adjacent areas of about 100 km on both sides of the border. This means the study area in Uruguay encompasses the departments Artigas, Salto, Rivera, Cerro Largo, Treinta y Tres, Rocha and part of Tacuarembó (north of National Route 26); in Brazil, the area comprises about the southern third of Rio Grande do Sul: to the north, it is delimited by the Ibicui River following its mouth up to Rosário do Sul; from there following Route BR 290 to the crossing with Route BR 392 near Caçapava do Sul, and to the east following Route BR 392 up to the Atlantic Ocean (Fig. 2). The following Brazilian municipalities are included (in alphabetical order): Aceguá, Alegrete, Arroio Grande, Bagé, Barra do Quaraí, Caçapava do Sul, Candiota, Canguçú, Capão do Leão, Cerrito, Chui, Dom Pedrito, Herval, Hulha Negra, Jaguarão, Lavras do Sul, Manoel Viana, Morro Redondo, Pedras Altas, Pedro Osório, Pelotas, Pinheiro Machado, Piratiní, Quaraí, Rio Grande, Rosário do Sul, Santa Margarida do Sul, Santa Vitória do Palmar, Santana da Boa Vista, Santana do Livramento, São Gabriel, São Sepé, Uruguaiana, and Vila Nova do Sul.

There are four main biomes occurring in the study area (Fig. 2):

(1) The eastern Atlantic coastal zone from Rio Grande in the North (Brazil) to Garzón lagoon in the South (Uruguay), which consists of a homogeneous environment of sand dunes and/or a special type of xerophytic vegetation. Aquatic habitats frequently used by amphibians are ponds with sandy or rocky bottom and stream margins. This environment is mainly affected by tourism and growing villages.

(2) Grassland or pampas, the main environment, where the predominant economical activities are developed until some years ago, i.e. cultivation of cattle (mainly cow and sheep) and crop (rice, soybean, wheat).

(3) Low hill ranges or hill formations, locally named "cuchillas", "coxilhas" or "sierras" (e.g. Cuchilla de Haedo, Cuchilla Negra, Cuchilla Santa Ana, Sierra de San Miguel). This macrohabitat consists of elevated land between 200 to 500 m a.s.l. with thin soil layer providing many lentic and lotic water bodies, i.e. streams and brooks. Most of the Cuchillas were originally covered by native forest, but today forestation with exotic species is mainly developed in this environment.

(4) In the East and Southeast of our study area, adjacent to the coastal zone, the landscape is dominated by wetlands. Although many of these humid habitats are conservation units, as in the case of the biosphere reserve "Humedales del Este" (Rocha, Uruguay) or "Estação Ecológica do Taim" (Rio Grande do Sul, Brazil), agriculture has rapidly grown in the last years. Many hectares in these wetlands, being rich in amphibian species diversity and abundance of individuals, had been drained in the last decade to provide place to crops (mainly rice and forage for cattle).

2.2 Data acquisition

The basic information on species distribution derives from specimens stored in regional collections and from published articles. For Brazilian localities, we included all records vouchered in the following collections: Fundação Zoobotánica do Rio Grande do Sul, Museu de Ciência e Tecnología da Pontifícia Universidade Católica do Rio Grande do Sul, Universidade Federal de Santa María and Universidade Federal do Rio Grande do Sul. For Uruguay, we used data provided by Núñez et al. (2004), which included material from the Colección de Zoología Vertebrados, Facultad de Ciencias (Uruguay), Museo Nacional de Historia Natural y Antropología (Uruguay) and the Uruguayan specimens stored in the Colección Herpetológica of Instituto Nacional Malbrán (now in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"). As Núñez et al. (2004) cited only specimens catalogued until August 2001, complementary data for additional specimens indexed until December 2005 were taken from ZVCB collection. Also individuals housed in European collections were included (i.e. SMNS).

In order to get more information, we reviewed all published papers and secondary literature (books, congress abstracts) relevant for the species of Bufonidae distributed in the border region. However, citations without voucher specimens (e.g. Braun

& Braun 1980) were not used for mapping the species distribution. Additional data were collected during 13 field trips between October 2001 and April 2006, where we visited the following localities:

- 4.–9.II.2002 – A. Kwet, R. Maneyro, J. Melchiors, T. Miranda, D. Naya and M. Solé (Rivera department: Rivera city, Masoller, Lunarejo, COFUSA; Rio Grande do Sul state: Santana do Livramento, Quaraí).
- 6.–8.V.2002 – R. de Sá, R. Maneyro, D. Naya and D. Núñez (Rivera department: Rivera city, COFUSA).
- 18.–20.IX.2002 – M. Beheregaray and R. Maneyro (Rocha department: Perla de Rocha, Oceanía del Polonio).
- 30.X.–2.XI.2002 – I. da Rosa, A. Kwet, R. Maneyro and M. Solé (Artigas department: Bella Unión; Salto department: Villa Constitución; Rio Grande do Sul state: Barra de Quaraí).
- 21.–25.IX.2003 – A. Camargo, A. Canavero and R. Maneyro (Tacuarembó department: Valle Edén).
- 19.–25.X.2003 – A. Kwet, R. Maneyro and D. Mebs (several localities in Rivera, Artigas, Cerro Largo, Treinta y Tres and Rocha departments).
- 7.–9.XI.2003 – A. Camargo, A. Canavero, I. da Rosa and R. Maneyro (Rivera department: Parque Gran Bretaña).
- 21.–23.XI.2003 – A. Canavero, R. Maneyro and D. Núñez (Rivera department: COFUSA, Route 27).
- 13.–22.I.2004 – M. Beheregaray and R. Maneyro (Rocha department: La Paloma, Cabo Polonio).
- 2.–4.II.2004 – A. Canavero, R. Maneyro and D. Naya (Cerro Largo and Treinta y Tres departments: Santa Clara del Olimar, Paso Pereira).
- During 2005 – M. Beheregaray, M. Di-Bernardo and R. Maneyro (Rivera department: Barrio Modelo, Campo del Abasto, Cuchilla Negra, Parque Gran Bretaña, Paso Ataques, Valle Platón).
- 10.–14.IV.2006 – M. Beheregaray, M. Brandimarti, R. Maneyro and D. Núñez (Rivera department: Campo del Abasto, Cuchilla Negra, Parque Gran Bretaña, Cerro Chapeu).
- 17.–20.IV.2006 – M. Beheregaray, N. Maciel and R. Maneyro (Rivera department: Campo del Abasto, Cerro Chapeu, Lagos del Norte).

3 General taxonomic comments

The family Bufonidae is one of the most widespread anuran families, with more than 450 valid species in almost 50 genera (Frost et al. 2006; Pramuk 2006). Among these genera, two are present in our study area: *Chaunus* Wagler, 1828 and *Melanophryniscus* Gallardo, 1961. According to the recent nomenclatural changes proposed by Frost et al. (2006), all species in this region previously placed in the genus *Bufo* Laurenti, 1768, are referred now to the revalidated genus *Chaunus* (see Frost 2006 and Frost et al. 2006 for nomenclatural comments). The definition of phenetic groups among the species of *Chaunus* follows Duellman & Schulte (1992).

The genus *Melanophryniscus* was described by Gallardo (1961c), based on three species, i. e. *M. stelzneri* (type species), *M. tumifrons*, and *M. moreirae*. The genus is currently represented by 20 species distributed in southern South America (Baldo & Basso 2004; Kwet et al. 2005; Di-bernardo et al. 2006). Uruguay and Rio Grande do Sul are considered the distribution centers of *Melanophryniscus* by Kwet et al. (2005). In Rio Grande do Sul, the genus is represented by at least eight species belonging to the *M. stelzneri* and *M. tumifrons* groups, and the recently described *M. admirabilis* which is not assigned to any group (Di-bernardo et al. 2006). In Uruguay, there are seven species, i. e. three in the *M. tumifrons* group, two in the *M. stelzneri* group and two in the *M. moreirae* group. Out of these, six species are found in the study area. The definition of groups in *Melanophryniscus* followed Caramaschi & Cruz (2002), Cruz & Caramaschi (2003) and Larson et al. (2003), who defined three, respectively four, phenetic groups in this genus, based on external morphology and colouration. However, a synapomorphy (frontal swelling) has been proposed only for the *M. tumifrons* group (Baldo & Basso 2004).

4 Results and discussion

4.1 Commented taxonomic list

A list of all bufonid species known to date from the border region between Uruguay and Rio Grande do Sul is given in Tab. 1. This checklist confirms the presence of two genera and 13 species of Bufonidae, with seven taxa belonging to the genus *Chaunus* and six to *Melanophryniscus*. Among them, five species of *Chaunus* and three of *Melanophryniscus* are found both in Uruguay and southern Rio Grande do Sul. Two species of *Chaunus* (*C. ictericus*, *C. henseli*) are widely distributed in southern Brazil, but not known from Uruguay; their localities in Rio Grande do Sul represent the southernmost distribution limit. On the other hand, there are three species of *Melanophryniscus*, which to date are only known from Uruguay and could be endemic to this country (*M. devincenzii*, *M. sanmartini*, *M.* sp.). However, *M. devincenzii* is controversially treated, due to the citation of an allopatric population in the Argentinean province Misiones, about 400 km to the northeast (Baldo & Krauczuk 1999), which in fact should belong to an undescribed species (see comments below). The overall species richness of Bufonidae in the study area is remarkably high. The recorded toads account for more than 90 % of the taxa in this family known from Uruguay and for about 55 % of the species occurring in Rio Grande do Sul.

4.1.1 *Chaunus dorbignyi* (Duméril & Bibron, 1841)

Bufo d'Orbignyi Duméril & Bibron, 1841. Holotype: MNHNP 4960. Type locality: "Montévidéo" (Montevideo, Uruguay).
Chilophryne d'orbignyi – Fitzinger 1843.
Bufo D'Orbignyi – Bibron 1847.
Bufo Orbignyi – Bibron 1847.
Bufo orbignyi – D'Orbigny 1847.

Bufo d'orbignyi – Günther 1859.
Bufo dorbignyi – Cope 1885.
Bufo Dorbignyi – Boulenger 1886.
Bufo globulosus d'orbignyi – Parker 1935.
Bufo granulosus d'orbignyi – Müller & Hellmich 1936.
Bufo granulosus – Freiberg 1942.

Material examined

Brazil (Rio Grande do Sul): Jaguarão: MCN 1146, 26/39. VIII.1975. – Pelotas: MCN 9009–9017, 21/27.IX.1975. – Rio Grande: MCN 10400–10409 and 10500–10509, Cassino, 20/25. VIII.1976. MCN 10642–10653, Taim, 29.VIII.1976. MCN 13382 and 13394, Taim, 26/30.IX.1988. – Santa Vitória do Palmar: MCN 10301–10309, 20 km depois do Farol Sarita, 20/26. VIII.1976. MCN 10597–10626 and 10628–10641, 25 km depois do Farol Sarita, 20/25.VIII.1976. MCN 10687–10690, 25 km depois do Farol Sarita, 25/29.VIII.1976. ZVCB 3956–3958, Alvorada, Barra do Chui, 15.I.2000.

Uruguay: **Artigas**: ZVCB 782, 6 km NNW de Belén, 1963. MNHN 4093, Barra del Arroyo Yacui, 10.I.1963. ZVCB 16, Barra del Arroyo Yacaré (CALNU), I.1952. ZVCB 398, Bella Unión, II.1952. ZVCB 2419, Bella Unión, XI.1960. ZVCB 1290, Desembocadura del Río Cuareim, II.1965. MNHN 1536, Río Cuareim, Sepulturas, 20.XII.1965. ZVCB 171, Próximo Arroyo Catalán chico, Estación Chilo Martínez, 30.I.1960. – **Cerro Largo**: MNHN 4062, 6 km SE de Melo, 20.II.1963. – **Rivera**: ZVCB 10665, Arroyo Rubio Chico, Ruta 30, 20/22.X.2003. ZVCB 797, Proximidades Arroyo Cuñapirú, 1.III.1969. – **Rocha**: MNHN 4202, Arroyo Chuy, 24.II.1984. MNHN 4184 and 4196, Chuy, 31.I.1984. ZVCB 1711, Coronilla, 3.I.1981. MNHN 364, Coronilla, XII.1954. ZVCB 2774, Coronilla, 17.X.1991. ZVCB 1179, La Paloma. MNHN 1256, Parque Nacional San Miguel, 26.VII.1964. ZVCB 3749, Parque Nacional Santa Teresa, 15.II.1999. MNHN 4209, Vivero Cabo Polonio, 1.XI.1970. – **Tacuarembó**: ZVCB 3059–3062, Paso Baltasar, 5.X.1996. ZVCB 2248–2252, Pueblo Ansina, 24.XI.1968. – **Treinta y Tres**: MNHN 612, Arroyo Los Membrillos, 24.VIII.1958. ZVCB 393, Arrozal 33, 1941. MNHN 4153, La Charqueada, 5.XI.1967. ZVCB 448, Santa Clara de Olimar, 1.XII.1957.

Taxonomic comments

This species in the *Chaunus granulosus* group was also considered a subspecies of either *C. granulosus* (Müller & Hellmich 1936; Cochran 1955) or *B. globulosus* (= *C. granulosus*; Parker 1935) (see Narvaes 2003). Following Berg (1896), Parker (1935) mentioned that the name *B. globulosus* has priority over *C. granulosus*, meaning that all taxa in the *granulosus* group must be considered subspecies of *B. globulosus*. Hence, Parker (1935) cited *Bufo globulosus d'orbignyi* as the correct taxon name, but Cei (1972) recognised *Bufo dorbignyi* as a valid species, which is now generally accepted (e. g. Achaval & Olmos 2003). In literature, there are several errors in the correct spelling of the species name, which was nominated in honor of Alcide D'Orbigny, because of the unjustified latinisation of his surname (Bibron 1847; D'Orbigny 1847; Günther 1859).

The type locality of this species was originally given as "Montévidéo", but a few years later corrected to "Maldonado" (D'Orbigny 1847). Based on the morphology of specimens collected at several localities (among them Maldonado and Montevideo), Gallardo (1957) followed this assumption and restricted the type locality to Maldonado. However, the arguments of Gallardo (1957) were not accepted by subsequent authors (Klappenbach & Langone 1992; Narvaes 2003), and again the type locality for this taxon is given as "Montevideo".

Tab. 1. Checklist of the species of Bufonidae Gray, 1825 in the border region between Uruguay and Brazil; summarised data from collection surveys, bibliographic revisions and fieldwork from 2002–2005.

Species	Brazil	Uruguay
***Chaunus granulosus* group**		
Chaunus dorbignyi (Duméril & Bibron, 1841)	X	X
Chaunus fernandezae (Gallardo, 1957)	X	X
***Chaunus marinus* group**		
Chaunus achavali (Maneyro, Arrieta & de Sá, 2004)	X	X
Chaunus arenarum (Hensel, 1867)	X	X
Chaunus ictericus (Spix, 1824)	X	
Chaunus schneideri (Werner, 1894)	X	X
***Chaunus crucifer* group**		
Chaunus henseli Lutz, 1934	X	
***Melanophryniscus stelzneri* group**		
Melanophryniscus atroluteus (Miranda-Ribeiro, 1920)	X	X
Melanophryniscus montevidensis (Philippi, 1902)	X	X
***Melanophryniscus moreirae* group**		
Melanophryniscus sp.		X
Melanophryniscus sanmartini Klappenbach, 1968b		X
***Melanophryniscus tumifrons* group**		
Melanophryniscus devincenzii Klappenbach, 1968b		X
Melanophryniscus pachyrhynus (Miranda-Ribeiro, 1920)	X	X

Geographical range

Argentina (mainly Buenos Aires, La Pampa and Río Negro provinces); Brazil (southeastern and eastern Rio Grande do Sul); Uruguay.

Conservation status

The populations in Uruguay and Rio Grande do Sul are considered "Not Endangered" (Maneyro & Langone 2001; García & Vinciprova 2003). At global level this species is classified as "Least Concern" (IUCN et al. 2006).

Natural history

The typical habitat of *C. dorbignyi* (Fig. 3) is characterised as "Pampas" (Narvaes 2003), but as mentioned above, its distribution range broadly overlaps with that of

C. fernandezae (Fig. 4), which is more typical for the "Coxilhas" (low hills) macrohabitat. Both species excavate small hollows in the ground, where the toads remain during periods of inactivity (Gallardo 1957). Their diet consists in arthropods, mainly ants and orthopterans (Gallardo 1974a; Isacch & Barg 2002). Stomach contents of specimens from southern Uruguay (referred to as "*Bufo gr. granulosus*") revealed that during the warm season *C. dorbignyi* feeds mainly on ants, whereas the diet spectrum seems to be wider in the cold season (Da Rosa et al. 2002). As stated by Langone (1995), most bibliographical references on larval morphology for *C. dorbignyi* might be based on specimens of *C. fernandezae*. However, the tadpole of *C. dorbignyi* was recently described from specimens from southern Uruguay (Borteiro et al. 2006a). Bioacoustic parameters of a male from Uruguay are given in Narvaes (2003).

Chaunus dorbignyi seems to hybridise with *C. fernandezae* in areas of contact between both species in Uruguay, Rio Grande do Sul and Buenos Aires (Gallardo 1965a, 1969; Narvaes 2003). According to Gallardo (1974a) and to the distribution maps of Global Amphibian Assessment (IUCN et al. 2006), there are two contact zones in our study area, one in the western part (northern Artigas, Barra de Quarai and Uruguaiana) and another in the eastern part (Pelotas and Rio Grande). However, according to Narvaes (2003) and our present data (Fig. 5), the region of overlap between both species seems to be more extended, including Artigas and Rivera in Uruguay, and Barra de Quarai, Uruguaiana and Santa Ana do Livramento in Brazil.

4.1.2 *Chaunus fernandezae* (Gallardo, 1957)

Chilophryne d'orbignyi – Jiménez de la Espada 1875.
Bufo Orbignyi – Cordero 1919.
Bufo d'orbignyi – Cordero 1933.
Bufo granulosus – Freiberg 1942.
Bufo granulosus d'orbignyi – Cochran 1955.
Bufo granulosus fernandezae Gallardo, 1957. Types: originally a set of 35 specimens (MACN 2389), but Gallardo (1965a) designated a male (now MACN 10334) in this series as type (= lectotype) and a female (now MACN 10335) as "allotype" (= one individual out of 34 paralectotypes). Type locality: "Bella Vista (Prov. de Buenos Aires, Argentina)" (Bella Vista, Buenos Aires Province, Argentina).
Bufo fernandezae – Cei 1964.
Bufo aff. *fernandezae* – Langone 1999.

Material examined

Chaunus fernandezae

Brazil (Rio Grande do Sul): Alegrete: UFRGS 2257–2263, Reserva Biologica Ibirapuita, 30.I.2001. – Barra do Quaraí: UFRGS 2241, Parque Espinilho, 2/4.II.2002. – Uruguaiana: UFRGS 1766–1768, XI.1997. MCT 7591–7592, Campus PUCRS, 2003. MCT 1854–1855, Fazenda Santo António, BR 472, km 40, 1996.

Uruguay: **Artigas**: MNHN 1262, 6 km NNW de Belén, 12.I.1963. ZVCB 779, 6 km NNW de Belén, 1963. ZVCB 1608, Arrocera Conti, 25.IX.1979. ZVCB 2052, Arrocera Conti, 23.IX.1982. ZVCB 3144, Arrocera Conti, 5.XII.1982. ZVCB 3238, Arrocera Conti, 20.VII.1982. ZVCB 3025, Arrocera Conti, Colonia Palma, 3.X.1996. MNHN 4060, Arrocera Conti, Colonia Palma, III.1959. ZVCB 1675, Arroyo Itacumbú, 180 m de barra en Río Uruguay, 23.VIII.1977. ZVCB 2247, Arroyo Itacumbú, 1,7 km de desembocadura, 19.VIII.1977. ZVCB 2334–2335, Arroyo Itacumbú, 1,7 km de desembocadura. ZVCB 10462–10464, Arroyo Yacaré, Azucarera CALNU, 1.I.1999. MNHN 4083 and 4085, Barra del Arroyo Yacui, 12.I.1963. MCT 6494–6495, Bella Unión, 2002. MNHN 4090, Bella Unión, 6.II.1965. ZVCB 2419, Bella Unión, XI.1960. ZVCB 10258–10260, Desembocadura del Río Cuareim, 1.I.2002. – **Cerro Largo**: MNHN 3131, 20 km de Pácido Rosas, 22.II.1982. – **Rocha**: MNHN 4152, Chuy, V.1984. – **Salto**: ZVCB 1580, Arrocera RIUSA, 5.X.1976. ZVCB 1595, Arroyo Algarrobo, Ciudad de Salto, 24.IX.1979. ZVCB 1016, Ciudad de Salto, 5.VIII.1970. ZVCB 1586, Constitución, 20.VIII.1979. ZVCB 1623, Constitución, 6.XI.1979. ZVCB 1630, El Espinillar, 25/28.X.1979. ZVCB 1702, El Espinillar, 22.VIII.1980. ZVCB 2087, El Espinillar, 24.IX.1982. ZVCB 1522, Rio Arapey Grande, 4 km de las Termas, 26.III.1978. ZVCB 2332, Rio Arapey Grande, 4 km de las Termas, 15.III.1972. ZVCB 1348, Termas de Arapey, 31.III.1971.

Chaunus aff. *granulosus*
(*Chaunus dorbignyi* × *Chaunus fernandezae*)

Brazil (Rio Grande do Sul): Capão do Leão: MCT 7510, Horto Botanico Ir Teodoro Luis, 2003. – Piratini: UFRGS 795, II.1968. UFRGS 801, II.1968. – Rio Grande: UFRGS 260, Taim, 18/22.VII.1981. – Uruguaiana: UFRGS 1769, XI.1997.

Uruguay: **Artigas**: MNHN 6024, Arrocera Conti, 20.VI.1987. ZVCB 1680, Arrocera Conti, 27.X.1980. ZVCB 3921–3922, Arroyo Itacumbú, 1,7 km de desembocadura, 24.VIII.1977. – **Cerro Largo**: ZVCB 772, Arroyo del Cordobés, 40 km del Río Negro, 1963. ZVCB 10936, Paso Pereira, 7.II.2004. ZVCB 10950, Paso Pereira, 2/10.II.2004. MNHN 6711, Paso Real, Río Yaguarón, 16.X.1999. ZVCB 10931, Santa Clara del Olimar al E de Ruta 7, 2.II.2004. – **Rivera**: ZVCB 10876, Minas de Corrales, 10/13. XII.2003. – **Rocha**: MNHN 6703, Aguas Dulces, 28.XII.1998. ZVCB 1514, Cabo Polonio, II.1977. MNHN 6334, Coronilla, 6.XII.1987. ZVCB 10720–10721, Entrada a Potrerillo, Laguna Negra, 24.X.2003. ZVCB 10937, Estación de Limnología, N de la Laguna de Rocha, 14.II.2004. – **Salto**: ZVCB 1562, Ciudad de Salto, 21.IX.1978. – **Tacuarembó**: ZVCB 10578–10581, Valle Edén, 21/25.IX.2003. – **Treinta y Tres**: MNHN 6569, Arrozal 33, 16/20.IX.1991.

Taxonomic comments

This species, the second taxon of the *Chaunus granulosus* group in our study area, is morphologically very similar and closely related to *C. dorbignyi* (see Narvaes 2003). In the original description, this taxon was treated as a subspecies of *C. granulosus* (Gallardo 1957), but later elevated to specific rank by Cei (1964). Currently this status is widely accepted (Achaval & Olmos 2003; Narvaes 2003; Brusquetti & Lavilla 2006), although there are many specimens with overlapping characteristics between

C. dorbignyi and *C. fernandezae*. See comments on hybridisation under *C. dorbignyi*.

Geographical range

Central and eastern Argentina (Buenos Aires, Córdoba, Corrientes, Chaco, Entre Ríos, Formosa and Santa Fé provinces); southeastern Brazil (central, western, and southeastern Rio Grande do Sul, and extreme south of Santa Catarina); Paraguay; Uruguay.

Conservation status

The populations in Uruguay and Rio Grande do Sul are considered "Not Endangered" (Maneyro & Langone 2001; García & Vinciprova 2003). At global level, this species is classified as "Least Concern" (IUCN et al. 2006).

Natural history

The typical habitat of *Chaunus fernandezae* (Fig. 4) has been characterised as "Coxilhas" (low hills) by Narvaes (2003), but its distribution range overlaps with that of *C. dorbignyi* in the "Pampas" biome (Figs. 3, 5). Both species are ecologically similar, living in small caves (Gallardo 1957) or individual hollows (Alcalde & Rosset 2004). The diet of *C. fernandezae* consists mainly of Hymenoptera (Basso 1990; Langone 1999; Woodhead & Maneyro 2003), although in toads from Argentina other groups of insects and arachnids predominated (Gallardo 1987). The colubrid *Liophis anomalus* and various raptor birds (kites, falcons, and owls) are cited as main consumers in nature (Gallardo 1987; Langone 1999; Rosset & Alcalde 2004). As in the case of *C. dorbignyi*, *C. fernandezae* is an "explosive breeder". Its reproductive activity occurs during the day or night and adult females contain up to 15.000 mature eggs (Basso 1990), which are deposited in large egg strings (Achaval & Olmos 2003). Sonograms and call parameters from Argentinean specimens are published in Straneck et al. (1993), Salas et al. (1998), and Narvaes (2003). Data on larval morphology are provided in Fernández (1927), Kehr & Williams (1990) and Lavilla et al. (2000a). A high variability in metamorphosis timing as a response to larval density and food level has been reported under experimental conditions (Kehr 1985). *Chaunus fernandezae* was considered as one of the poisonous toad species inhabiting Rio Grande do Sul (Braun 1978), who referred to this species as "*Bufo granulosus fernandezae*".

4.1.3 *Chaunus achavali* (Maneyro, Arrieta & de Sá, 2004)

Bufo achavali Maneyro, Arrieta & de Sá, 2004. Holotype: ZVCB 3779. Type locality: "Outskirts of Pueblo Valentines. Departamento de Treinta y Tres, Uruguay".

Material examined

Brazil (Rio Grande do Sul): Caçapava do Sul: MCN 9133–9135, 28/30.X.1975. ZUFSM 3364–3365, Guaritas, 3.I.2003. – Candiota: MCT 3936–3941, 1999. MCT 3973, 2000. MCT 4095, 2000. MCT 4374–4375, 2001. MCT 4466–4468, 2001. UFRGS 1007–1008, 6.III.1988. – Pedro Osório: UFRGS 884, 1/11.II.1966.

Uruguay: **Artigas**: ZVCB 77, Arroyo de la Invernada, II.1954. ZVCB 84, Arroyo de la Invernada, II.1954. – **Rivera**: ZVCB 8240 and 8242, Campo San Juan (Campos de COFUSA), 15.XII.2001. ZVCB 8371, Est. Trinidad, 12/14.X.2001. ZVCB 8603, Est. Velázquez, 10/12.XI.2001. ZVCB 8229, Estancia Capón Alto (Campos de COFUSA), 18.VIII.2001. ZVCB 3331, Sierra de la Aurora, 12/26.I.1971. – **Tacuarembó**: ZVCB 271a, Gruta de los Cuervos, 18.XII.1952. – **Treinta y Tres**: ZVCB 3815, Arroyo Yerbal Grande, 29.III.1999. ZVCB 3801, Estancia Doña Alba, 16 km NW de Isla Patrulla, 12.V.1999 (paratype). ZVCB 4031, Estancia Doña Alba, 16 km NW de Isla Patrulla, 10.IV.1999. ZVCB 4727, Estancia Doña Alba, 16 km NW de Isla Patrulla, 1999. ZVCB 3779, Proximidades de Pueblo Valentines, 1998 (holotype).

Taxonomic comments

The original description placed this species in the *Chaunus marinus* group (Maneyro et al. 2004). Morphologically, it is closely related to *C. arenarum* Hensel, 1867 and *C. rubescens* Lutz, 1925 (Maneyro & Arrieta 2000). The latter species was also treated under the synonymised taxon name *B. rufus* Garman, 1877, which is a primary homonym of *Bufo rufus* Schneider, 1799 [= *Bufo terrestris* (Bonnaterre, 1789)]; see discussion in Lavilla (1994).

Geographical range

Northern Uruguay (Fig. 6) and recently also cited from various localities in southern and central Rio Grande do Sul state (Kwet et al. 2006).

Conservation status

Uruguayan populations are considered "Endangered" (referred to as "*Bufo* sp." in Maneyro & Langone 2001). Status for Rio Grande do Sul and at global level not evaluated.

Natural history

This species inhabits lotic water bodies, e. g. brooks and forest streams among hills (Maneyro et al. 2004). Faeces of two specimens collected in Cerro Chapeu (Rivera department, Uruguay) contained parts of arthropods (mainly hymenopterans and coleopterans). Advertisement call and tadpole are unknown but, derived from dissected collection specimens and field observations, reproductive activity might occur between October and January (Kwet et al. 2006).

4.1.4 *Chaunus arenarum* (Hensel, 1867)

Leiuperus marmoratus – D'Orbigny 1847.

Bufo arenarum Hensel, 1867. Lectotype: ZMB 6779. –Hensel (1867) mentioned seven syntypes, but only three specimens

are still existent. ZMB 6779 was designated lectotype by Kwet et al. (2006), being ZMB 57370 and ZMB 57371 paralectotypes. Type locality: "bei der Stadt Rio-Grande do Sul", Brazil; this locality was restricted to Rio Grande (Rio Grande do Sul state) by Bokermann (1966).

Bufo agua – Cunningham 1871.
Bufo marinus var. platensis Jiménez de la Espada, 1875.
Phryniscus connectens Philippi, 1902.
Bufo arenarius – Lutz 1934.
Bufo arenarum platensis – Gallardo 1965b.
Bufo arenarum chaguar Gallardo, 1965c.

Material examined

Brazil (Rio Grande do Sul): Rio Grande: MCN 10288–10299, Cassino, 20/25.VIII.1976. MCN 5230, Taim, 22.XI.1979. UFRGS 20–29, Taim, 22/23.I.1979. UFRGS 30–31, Taim, 15.XII.1979. UFRGS 32, Taim, 12.III.1980. UFRGS 33–35, Taim, 18/19.IV.1980. UFRGS 36, Taim, 11.IX.1980. UFRGS 37–39, Taim, 25.II.1981. UFRGS 215, Taim, 13.XII.1979. UFRGS 216, Taim, 17.XII.1979. UFRGS 217–218, Taim, 5.XII.1980. SMNS 9111, Taim, 20.III.1996. ZMB 6779, Rio Grande (lectotype). ZMB 57370–57371, Rio Grande (paralectotypes). – Santa Vitória do Palmar: ZVCB 3955, Alvorada, Barra do Chui, 15.I.2000.

Uruguay: **Rocha**: MNHN 6699, Aguas Dulces, 28.XII.1998. ZVCB 143, Aguas Dulces, 9.III.1959. ZVCB 218, Aguas Dulces, 24.III.1963. ZVCB 3932, Aguas Dulces, 7.XII.1999. ZVCB 4836–4847, Aguas Dulces, 1.I.1998. ZVCB 4900, Barra de la Laguna de Rocha, 10.II.2001. MNHN 4014, Cabo Polonio, 5.XI.1983. ZVCB 29, Cabo Polonio, III.1955. ZVCB 165, Cabo Polonio, 16.I.1960. ZVCB 466, Cabo Polonio, III.1953. ZVCB 471, Cabo Polonio, 2.III.1956. ZVCB 748, Cabo Polonio, 5.II.1962. ZVCB 1654, Cabo Polonio, 17.XI.1980. ZVCB 1668, Cabo Polonio, 6.II.1980. ZVCB 1735–1736, Cabo Polonio, 11/13.I.1981. ZVCB 1745–1749, Cabo Polonio, 4.I.1981. ZVCB 1750–1751, Cabo Polonio, 21.II.1980. ZVCB 2225, Cabo Polonio, II.1960. ZVCB 4027–4030, Cabo Polonio, 1.II.1971. ZVCB 8243, Cabo Polonio, 13.II.1980. ZVCB 10431, Cabo Polonio, 15.I.2004. ZVCB 10932–10934, Cabo Polonio, 20.I.2004. ZVCB 827, Cabo Santa María, 9.XI.1968. ZVCB 1248, Costa Azul, 27.XII.1946. MNHN 469, La Coronilla, XII.1954. MNHN 2479, La Paloma, 3.I.1973. ZVCB 257, Laguna de Rocha, 25.II.1953. MNHN 6357, Laguna Negra, 10.X.1992. ZVCB 2217, Parque Nacional Santa Teresa, 8.I.1978. ZVCB 1443, Parque Nacional Santa Teresa, 1/11.II.1978. ZVCB 10444–10448, Playa La Calavera (Cabo Polonio), 22.I.2004. MNHN 2108, Punta del Diablo, III.1974. SMNS 11842, Punta del Diablo, 24.X.2003. ZVCB 1484, Punta del Diablo, 19.XII.1972. ZVCB 10682, Punta del Diablo, 24.X.2003. ZVCB 3306, Vivero Forestal, Cabo Polonio, 5.X.1985. – **Salto**: ZVCB 1569, Ciudad de Salto, 21.IX.1978. ZVCB 3459, Ciudad de Salto, Club de Remeros, 27.II.1998.

Taxonomic comments

Leiuperus marmoratus (= *Pleurodema marmoratum*) was described by Duméril & Bibron (1841), based on specimens from Potosí (Bolivia), but D'Orbigny (1847) stressed that this *taxon* inhabits artificial and natural water bodies in the surroundings of Montevideo, Uruguay. Later, *Leiuperus marmoratus* from Bolivia was placed in the genus *Pleurodema* Parker, 1927 and based on geographical distribution range (Montevideo) and morphological characteristics (colouration, skin texture) Klappenbach & Langone (1992) placed the Uruguayan population mentioned by D'Orbigny (1847) in the synonymy of *Bufo arenarum*. Among several other taxa, Philippi (1902) described *Phryniscus connectens*, figured in Cei (1958) and recognised as juveniles of *Bufo arenarum* by Klappenbach (1968a). The name *Bufo arenarius* mentioned by Lutz (1934) is an incorrect subsequent spelling (Klappenbach & Langone 1992).

The variety *B. arenarum* var. *platensis* Jiménez de la Espada, 1875, erroneously treated as a synonym of *B. marinus* by Savage (1978), was placed in the synomymy of *B. arenarum* by Boulenger (1882), but revalidated as a subspecies by Gallardo (1965b). However, Laurent (1969) did not recognise *B. a. platensis* and synonymised this taxon and another subspecies, *B. a. chaguar*, described by Gallardo (1965c), with *B. arenarum*. *Bufo mendocinus*, described from "Provinz Mendoza, bei Vistaflor, Argentina" by Philippi (1869), was treated as another subspecies by Gallardo (1964). This means, to date *C. a. mendocinus* Philippi, 1869 is the only valid subspecies (see Lavilla & Cei 2001). However, due to the distant and geographically well separated distribution areas (see IUCN 2006) it may be possible that in the future this taxon might be recognised at full species level.

Geographical range

Argentina (south to Chubut Province); Bolivia (for details see De la Riva et al. 2000); Brazil (eastern Rio Grande do Sul) and south and east of Uruguay.

Conservation status

Populations from Uruguay and Rio Grande do Sul are considered "Not Endangered" (Maneyro & Langone 2001; García & Vinciprova 2003) as well as those from Argentina (Lavilla et al. 2000b). At global level this species is classified as "Least Concern" (IUCN et al. 2006).

Natural history

Chaunus arenarum is one of the most common species in the coastal zones of Uruguay and Rio Grande do Sul (Langone 1995; Maneyro et al. 1995). This toad mainly inhabits sandy habitats (Fig. 7), but is also found in wetlands, near natural and artificial ponds, and close to anthropogenised environments (Langone 1999; Achaval & Olmos 2003). Diet analysis on Argentinean populations revealed mainly ants and coleopterans (Isacch & Barg 2002), but the diet may also include small vertebrates (Langone 1995). This species was observed feeding on the shoreline nearby the Atlantic Ocean (Achaval & Olmos 2003). The colubrid *Philodryas patagoniensis* is one of the most important predators in Uruguay (Carreira Vidal 2002). Bioacoustic analyses of the call of Argentinean specimens, including sonograms, are provided in Barrio (1964), Straneck et al. (1993), and Salas et al. (1998). Females produce up to 40.000 eggs which are arranged in

two strings. The tadpoles finish their metamorphosis about 30 days after spawning (LANGONE 1995). Morphological characteristics of the tadpoles are given in SCOTT-BIRABEN & FERNÁNDEZ (1921), ECHEVERRÍA et al. (1987), and CEI (1980), all referring to Argentinean populations. A description of the buccal apparatus and intestinal content of larvae is published in ECHEVERRÍA (1998). In the skin of adult *C. arenarum*, several venomous compounds were identified, among these bufotenine, dehydrobufotenine, bufothionine, bufotenidines, bufogenin, and bufalin (CEI et al. 1968; BRAUN 1978; CEI 1980; MEBS et al. 2007); whereas in tadpoles only dehydrobufotenine was found (MEBS et al. 2007).

4.1.5 *Chaunus ictericus* (Spix, 1824)

Bufo bimaculatus WIED-NEUWIED, 1821.
Bufo fuliginosus WIED-NEUWIED, 1821.
Bufo ictericus SPIX, 1824. Type: RMNH 2182, designated lectotype by HOOGMOED & GRUBER (1983). Type locality: "Provinciae Rio de Janeiro" (Rio de Janeiro State, Brazil).
Docidophryne icterica – FITZINGER 1861.
Bufo missionum BERG, 1896.
Bufo marinus ictericus – MÜLLER 1927.
Bufo ictericus mertensi COCHRAN, 1950.
Bufo ictericus ictericus – COCHRAN 1950.

Material examined

Brazil (Rio Grande do Sul): Caçapava do Sul: MCN 9133–9135, 28/31.X.1975. ZUFSM 3438, Guaritas, 8.II.2003.

Taxonomic comments

Prior to the original description of *Chaunus ictericus* by SPIX (1824), two other taxa were described by WIED-NEUWIED (1821), i. e. *B. bimaculatus and B. fuliginosus*. Without designating type specimens, the type locality of both species was given as "Serra de Inoã, Inoã, município de Maricá, Rio de Janeiro". Both taxa were considered "nomina oblita" and placed *in the synonymy of B. ictericus (see BOKERMANN 1966). Bufo missionum* Berg, 1896 was erroneously placed in the synonymy of *Bufo rufus* Garman, 1877 (= *Chaunus rubescens* Lutz, 1925; see comments under *B. achavali*) by GALLARDO (1961a), but must be considered a synonym of *C. ictericus* according to FAIVOVICH & CARRIZO (1997). *Chaunus ictericus* was for a long time treated as a synonym of *C. marinus*, but MÜLLER (1927) noted the striking differences in southeastern populations (e. g. longer parotoid glands and distinct colouration of females) and revalidated this taxon as subspecies *B. marinus ictericus*. Finally VELLARD (1948) elevated *B. ictericus* to full species rank.

The subspecies *B. ictericus mertensi* was described by COCHRAN (1950), based on specimens from Santa Catarina (Brazil). COCHRAN (1950) stated the nominal *B. i. ictericus* inhabiting São Paulo and Rio de Janeiro states and assigned *B. i. mertensi* to the southern populations (including Rio Grande do Sul) with type locality "Nova Teutonia, Itá, Santa Catarina". However, when comparing specimens of large series from Rio Grande do Sul and São Paulo, MÜLLER (1969) found no morphometric differences and concluded that this subspecies must be treated as a synomym. Populations from Bahia and Minas Gerais states, central Brazil, are currently re-evaluated and morphological differences seem to justify their description as a new taxon (BRANDÃO pers. comm.).

Geographical range

Northeastern Argentina (Corrientes and Misiones provinces); northeastern Paraguay; central to southern Brazil (south to central Rio Grande do Sul).

Conservation status

The populations in Rio Grande do Sul are considered "Not Endangered" (GARCÍA & VINCIPROVA 2003). At global level, the species is classified as "Least Concern" (IUCN et al. 2006).

Natural history

The northern parts of our study area mark the southernmost distribution limit of this species, and records (Fig. 8) are very scarce (only from Caçapava do Sul municipality). However, *Chaunus ictericus* is very common from northern Rio Grande do Sul (KWET & DI-BERNARDO 1999) to central Brazil, with its distribution extending along the Atlantic Rain forest domain (KWET & DI-BERNARDO 1999; STEVAUX 2002). The diet of this species in Rio Grande do Sul mainly consisted of coleopterans, ants and diplopods (BECKMANN 2003); larger prey, e. g. frogs or small mammals as reported for *C. marinus*, could not be observed in this study. The voice of this toad was described (without providing a sonogram) as "curúrúrúrú" (LUTZ 1954), from which the local name "Sapo Cururú" is derived. A sonogram is found in STRANECK et al. (1993). The reproductive mode of this toad is basal. Females in Rio Grande do Sul produced about 9.000 (maximum 13.000) melanistic eggs in egg strings with exotrophic tadpoles, which reached their metamophosis after two months (BECKMANN 2003). HADDAD et al. (1990) commented on natural hybridisation between *C. ictericus* and *C. crucifer* with fertilised eggs, but formation of teratological hybrids. A tadpole description of *C. ictericus* was given by ROSA (1965). This toad was listed as one of the amphibians with poisonous skin secretions in Rio Grande do Sul by BRAUN (1978), but no details about the chemistry of these venoms were published.

4.1.6 *Chaunus schneideri* (Werner, 1894)

Bufo schneideri WERNER, 1894. Holotype: NHMB 1916. Type locality: "Paraguay".
Bufo paracnemis LUTZ, 1925.
Bufo marinus paracnemis – MÜLLER & HELLMICH 1936.

Material examined

Brazil (Rio Grande do Sul): Alegrete: UFRGS 924, Harnesnia, 4.XI.1961. UFRGS 2238–2239 and 2253, Reserva Biologica Ibirapuita, 30.I.2001. – Barra do Quaraí: MCN 12171, XI.1977. – Manoel Viana: ZUFSM 2424, Costa del Rio Ibicuy, 16.IX.2000. – Rosário do Sul: MCT 5717, 2002. – Uruguaiana: MCN 6425–6431, XII.1973. MCT 3910, 1999. MCT 1964, BR 472, km 40, 1996.

Uruguay: **Artigas**: MNHN 2469–2470 and 4223, 11 km W Colonia Palma, 6.XII.1975. MNHN 1252, 6 km NNW de Belén, 10.I.1963. ZVCB 2259, 6 km NNW de Belén, 21.I.1963. MNHN 4048–4049, Arrocera Conti, IX.1979. ZVCB 1588–1592, Arrocera Conti, 24/25.IX.1979. ZVCB 1666–1667, Arrocera Conti, 25.I.1980. ZVCB 1737–1738, Arrocera Conti, 28.XII.1980. ZVCB 3145, Arrocera Conti, 5.XII.1982. ZVCB 3181, Arrocera Conti, 1.X.1976. ZVCB 3198, Arrocera Conti, XII.1982. ZVCB 3310, Arrocera Conti, 30.VI.1979. ZVCB 84, Arroyo de la Invernada, II.1954. ZVCB 2333, Arroyo Itacumbú, 1,7 km de la boca, 24.VIII.1977. ZVCB 1069, Arroyo Tres Cruces, I.1958. ZVCB 10465–10466, Arroyo Yacaré, Azucarera CALNU, 1.I.1999. MNHN 4227, Bella Unión, XII.1958. ZVCB 88, Bella Unión, II.1952. ZVCB 182, Bella Unión, XI.1960. ZVCB 406, Bella Unión, IV.1951. MNHN 6632, Colonia Palma, Ruta 30, 25.II.1980. ZVCB 1739, Hotel Calnu, 28.I.1981. ZVCB 903, Proximidades Bella Unión, III.1951. ZVCB 1062, San Gregorio, II.1960. ZVCB 2037, Yuquery, 1.II.1970. – **Salto**: ZVCB 1593, Arroyo Algarrobo al sur ciudad de Salto, 24.IX.1979. ZVCB 1619, Arroyo Algarrobo al sur ciudad de Salto, 28.X.1979. ZVCB 904, Ciudad del Salto, 15.XI.1969. ZVCB 1144, Ciudad de Salto, I.1972. ZVCB 1625, 1632 and 1640–1651, El Espinillar, 25/28.X.1979. ZVCB 1961–1962, El Espinillar, 28.XI.1981. ZVCB 3221–3223, El Espinillar, 9.III.1982. ZVCB 1568 and 1570, Laguna en la ciudad de Salto, 21.IX.1978. ZVCB 1477, Parador Quiroga, 19.X.1978. ZVCB 1146 and 1220, Río Arapey Grande, 4 km de las Termas, 16.III.1972. ZVCB 1145, Termas del Arapey, 10/20.III.1972. ZVCB 3950–2952, Villa Constitución, 27.XII.1999.

Taxonomic comments

Shortly after its description by Werner (1894), *Bufo schneideri* was synonymised by Boulenger (1895), due to the presumed homonymy with *Bufo schneideri* Merrem, 1820 (= *Lithodytes lineatus*). However, subsequently this turned out as erroneous by misinterpreting the taxonomic status of "*Rana schneideri*" (see discussion in Frost 2006). Until recently, *Bufo paracnemis* described by A. Lutz (1925) and based on specimens from "…l'etat de Minas" (restricted to Belo Horizonte by Bokermann 1966), was accepted as the valid species name for this toad (see discussion in Frost 2006), although Gallardo (1962) indicated this taxon should be treated as a junior synonym of *B. schneideri*. Populations from the Brazilian states of Bahia and Pernambuco, referred to this species by Cochran (1955), may actually belong to *C. jimi*, a taxon recently described by Stevaux (2002).

Geographical range

Northern and northeastern Argentina; Bolivia (east of the Andes); Paraguay; central, southern and southeastern Brazil; northwest of Uruguay.

Conservation status

Populations from Uruguay and Rio Grande do Sul are listed as "Not Endangered" (Maneyro & Langone 2001; García & Vinciprova 2003). At global level this species is considered as "Least Concern" (IUCN et al. 2006).

Natural history

This is the largest bufonid in the study area (Fig. 9) reaching up to 210 mm in females. The geographical distribution in Uruguay was originally restricted to the extreme northwest, in the surroundings of the Uruguay River (no more than 30 km to the east), but this species was recently introduced to some additional localities (Puntas de Cuñapirú, Rivera). These toads successfully coexist with human activities and reach great abundances in towns like Salto and Constitución (Salto department) or Bella Unión (Artigas department). In Rio Grande do Sul, the species is found in a wide range of different habitats. In nature, *C. schneideri* feeds mainly on insects, but may also engulf small vertebrates (Achaval & Olmos 2003). The reproduction takes place in natural and artificial lentic water bodies. Males call from different places under varying water depth conditions, e. g. at the pond margin or within the water. Females spawn thousands of eggs arranged in two strings attached to aquatic vegetation (Langone 1995). Descriptions of tadpoles are found in Rosa (1965), Vizotto (1967), and Cei (1980), descriptions of the buccal apparatus and intestinal content of larvae in Echeverría (1998). The poisonous skin compounds of *C. schneideri*, particularly in the parotoid and paracnemic glands, are strong enough to kill a dog (Langone 1995). Cei (1980) provided a table with data on concentrations of indolalkilamines, bufotenines, bufotenidines, and bufothionines in this species.

4.1.7 *Chaunus henseli* (Lutz, 1934)

Bufo crucifer var. henseli Lutz, 1934. Type: not designated in the original description. According to Baldissera et al. (2004), the holotype was "originally in the AL-MN collection, currently missing" [AL-MN = Collection of Adolfo Lutz, actually in the Museu Nacional de Rio de Janeiro]. Type locality: "São Bento, Estado de Santa Catarina" (Santa Catarina State, Brazil).

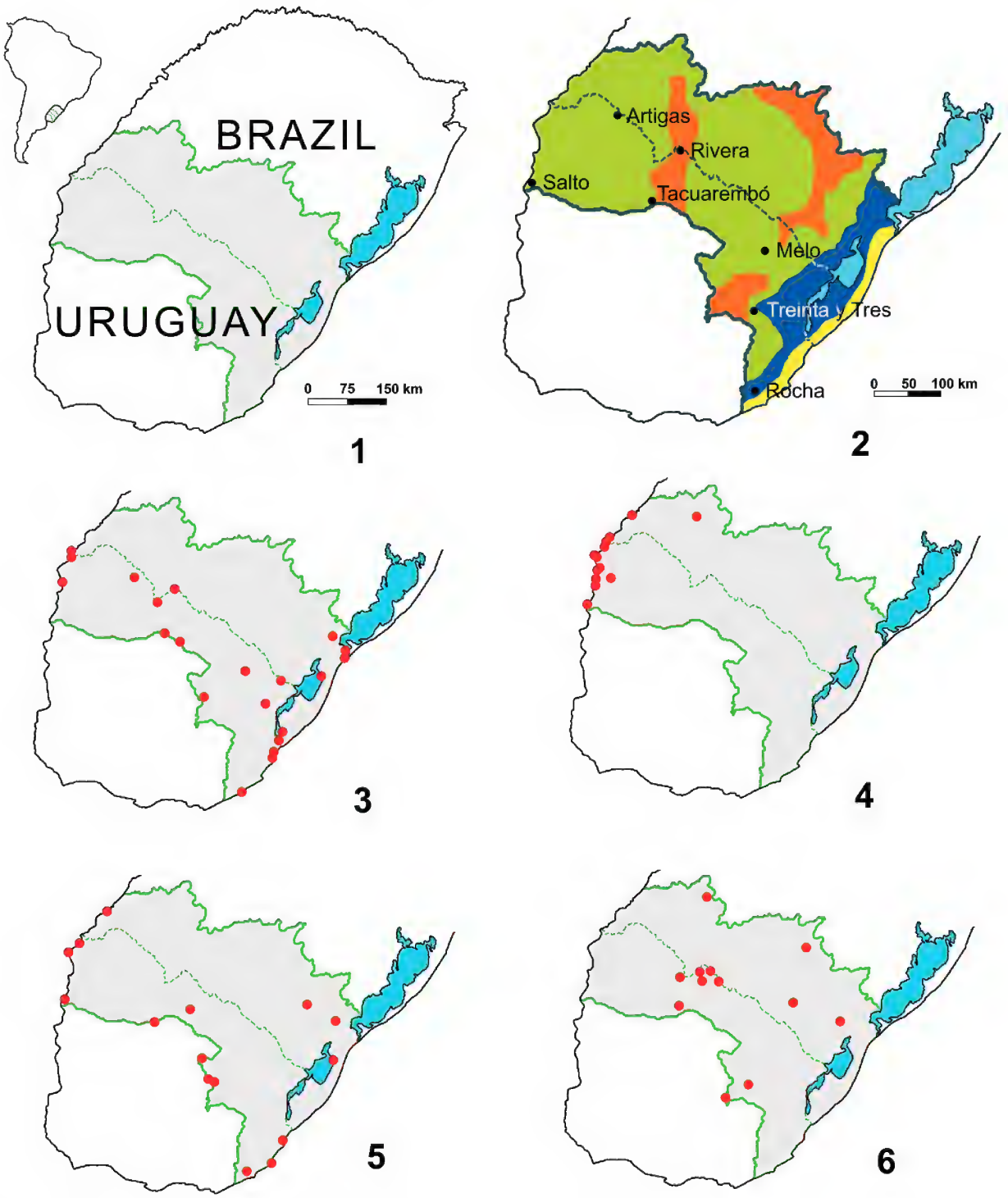
Bufo henseli – Baldissera et al. 2004. Although providing an accurate redescription including drawings and fotos of an adult male (MCN 9996 without specification of locality), the authors did not designate a neotype.

Material examined

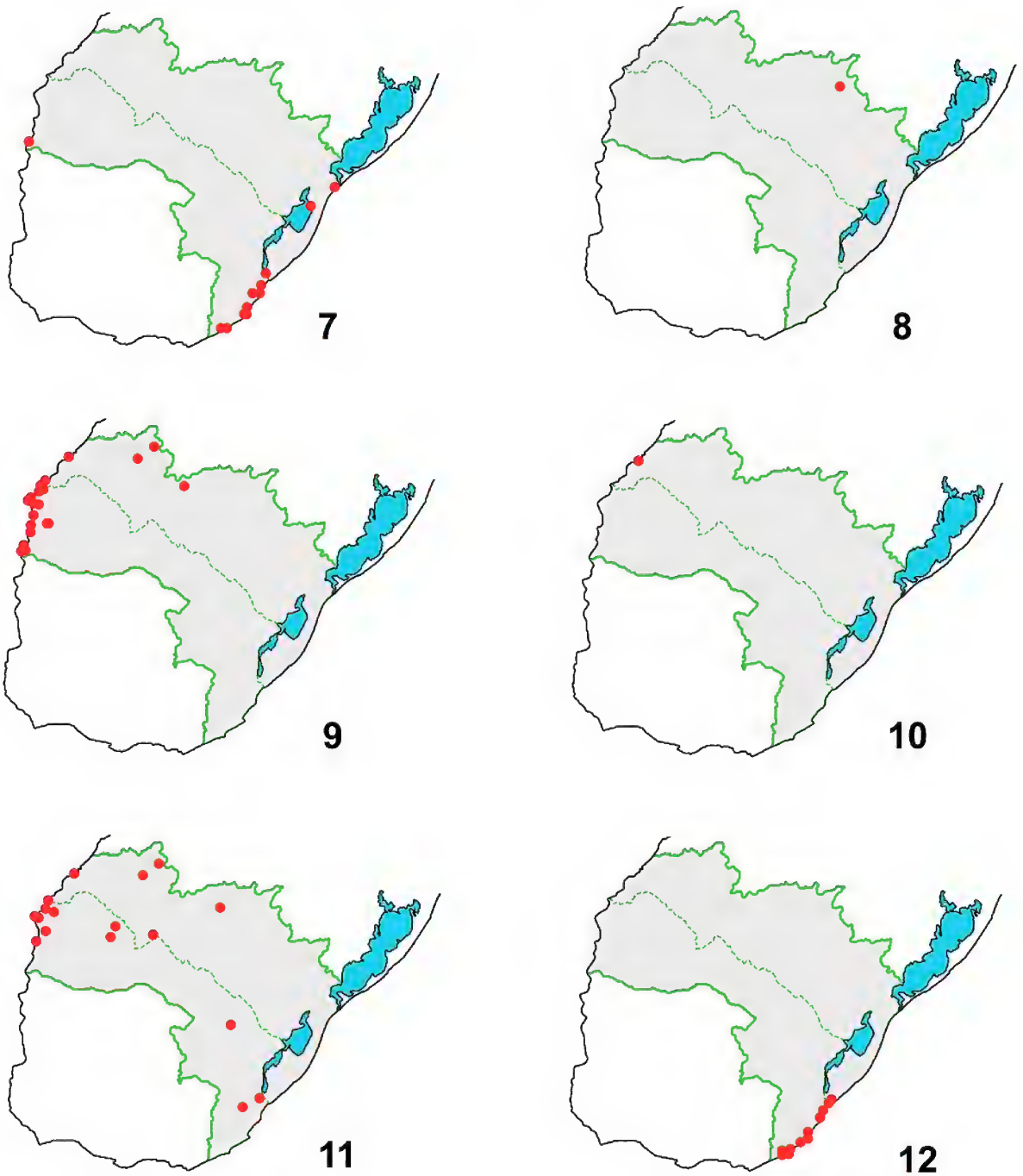
Brazil (Rio Grande do Sul): Uruguaiana: UFRGS 770, XI.1997.

Taxonomic comments

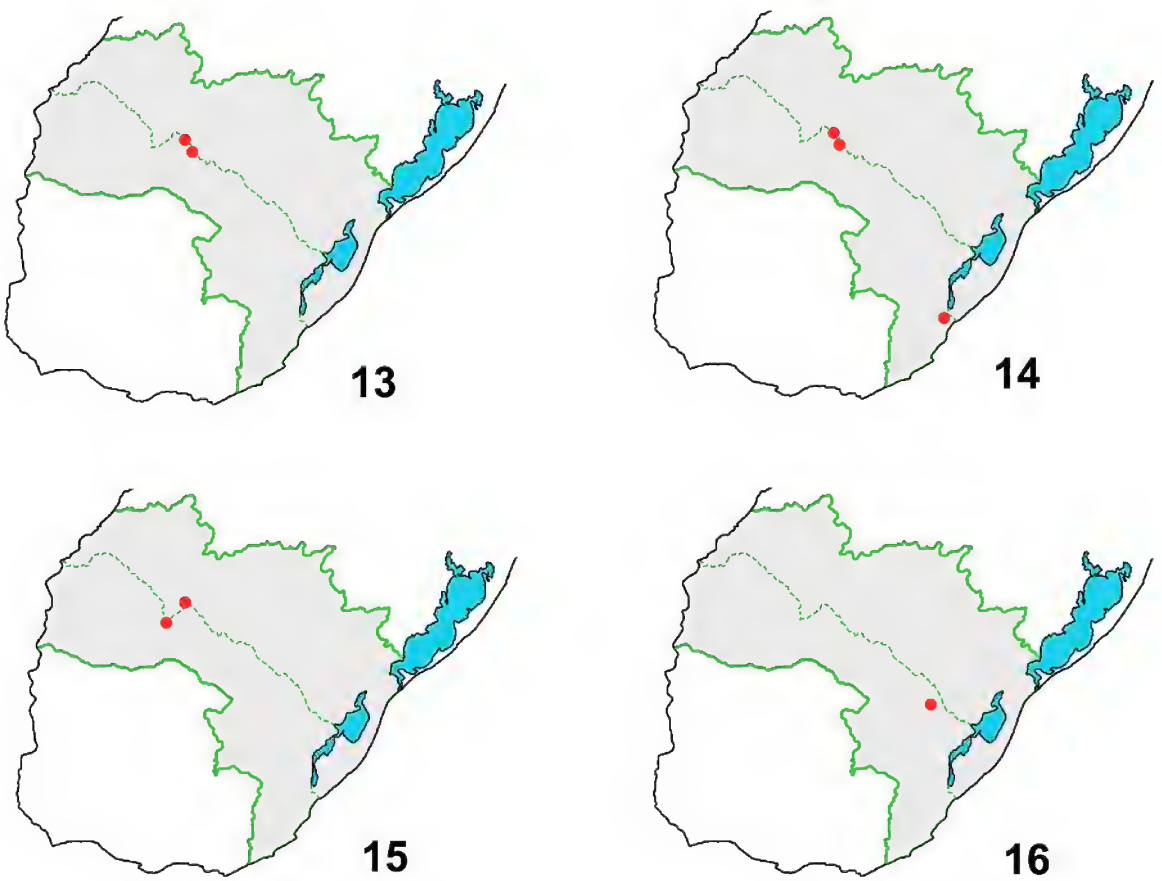
Bufo crucifer var. *henseli* Lutz, 1934 was described as a subspecies of *Bufo crucifer* (Wied-Neuwied, 1821) and



Figs. 1–6. Study region (1–2) and distribution maps of *Chaunus* spp. (3–6). – **1.** Location of the study area in southern South America. **2.** Study area along the border region between the Brazilian state of Rio Grande do Sul and Uruguay; major habitat types: grassland or pampas (green), low hill ranges (orange), wetlands (blue), Atlantic coastal zone with sand dunes (yellow). **3**. *Chaunus dorbignyi*. **4**. *C. fernandezae*. **5**. *C. dorbignyi* × *fernandezae*. **6**. *C. achavali*.



Figs. 7–12. Distribution maps of *Chaunus* spp. and *Melanophryniscus* spp. – **7**. *Chaunus arenarum*. **8**. *C. ictericus*. **9**. *C. schneideri*. **10**. *C. henseli*. **11**. *Melanophryniscus atroluteus*. **12**. *M. montevidensis*.



Figs. 13–16. Distribution maps of *Melanophryniscus* spp. – **13**. *M.* sp. **14**. *M. sanmartini*. **15**. *M. devincenzii*. **16**. *M. pachyrhynus*.

Figs. 17–22. *Chaunus* spp. – **17**. *C. dorbignyi* (photo Marcelo Casacuberta). **18**. *C. fernandezae* (photo Axel Kwet). **19**. *C. achavali*, male (photo Axel Kwet). **20**. *C. arenarum* (photo Axel Kwet). **21**. *C. ictericus*, female (photo Axel Kwet). **22**. *C. schneideri* (photo Axel Kwet).

Figs. 23–26. *Chaunus* and *Melanophryniscus* spp. – **23**. *Chaunus henseli*, female (photo Daniel Bühler). **24**. *Melanophryniscus* sp. (photo Diego Baldo). **25**. *M. sanmartini*, lateral (a) and ventral (b) view (photos Francisco Kolenc). **26**. *M. devincenzii*, dorsolateral (a) and ventral (b) view (photos Axel Kwet).

Figs. 27–29. *Melanophryniscus* spp. – **27**. *M. pachyrhynus*, lateral (a) and ventral (b) view (photos Axel Kwet). **28**. *M. atroluteus*, lateral (a) and ventral (b) view (photos Francisco Kolenc). **29**. *M. montevidensis*, dorsolateral (a) and ventral (b) view (photos Axel Kwet).

recently revalidated at full species level as *Bufo henseli* (now *Chaunus henseli*) by BALDISSERA et al. (2004). Because of the wide distribution range of the former *B. crucifer*, some authors had already suggested that this taxon may include more than one species (e. g. HADDAD & SAZIMA 1992). COCHRAN (1955) analysed *B. crucifer var. henseli* among other taxa synonymised with *B. crucifer* and suggested that more specimens were needed to draw wider conclusions. Recently, an exhaustive analysis of the *crucifer* group by BALDISSERA et al. (2004) provoked considerable taxonomical changes, i. e. besides the revalidation of *Bufo henseli* and *B. ornatus* (now *Chaunus henseli* and *C. ornatus* according to FROST et al. 2006), the authors described two new taxa, *B. abei* and *B. pombali* (now *C. abei* and *C. pombali* according to FROST et al. 2006).

Geographical range

This species occurring in the Brazilian states of Santa Catarina and Rio Grande do Sul was recently found also in adjacent Paraná (LIMA et al. 2005). Due to the geographical vicinity, this new record makes an occurrence of *C. henseli* in the Argentinean provinces Misiones and Corrientes highly probable, although BALDISSERA et al. (2004) stated the population of the *C. crucifer* group found in Argentina might belong to *C. ornatus*. However, up to date there are no confirmed records of *C. ornatus* in Paraná, and the occurrence of this species distributed further to the north seems unlikely in Argentina.

Conservation status

Chaunus crucifer was treated as "Not Endangered" in Rio Grande do Sul (GARCÍA & VINCIPROVA 2003) and "Least Concern" at global level (IUCN et al. 2006). However, this conservation status must be re-evaluated considering the taxonomical changes in this group.

Natural history

There is an apparently erroneous citation of the species for Uruguay (MIRANDA-RIBEIRO 1926), and up to date no specimens could be collected in this country. The single reference for our study area comes from Uruguaiana in western Rio Grande do Sul, close to the Uruguay River (Fig. 10). However, this citation needs to be confirmed, because the open grassland being characteristic for this region is not the preferred habitat for this forest species. A sonogram, treated as *B. crucifer* but presumably belonging to *C. crucifer*, is found in STRANECK et al. (1993). Observations on diet, reproduction and natural history were made based on populations belonging to *C. crucifer*, i. e. studies on diet composition and ecological effects of aggregating behaviour in tadpoles by ETEROVICK (2000). This taxon was listed as one of the poisonous toad species in Rio Grande do Sul by BRAUN (1978).

4.1.8 *Melanophryniscus atroluteus* (Miranda-Ribeiro, 1920)

Atelopus atro-luteus MIRANDA-RIBEIRO, 1920. Types: originally two specimens (MZUSP 814), actually syntypes MZUSP 814 and MZUSP 55577 (see KLAPPENBACH & LANGONE 1992). Type locality: "Estado do Rio Grande do Sul (Itaqui)" (Itaqui, Rio Grande do Sul State, Brazil).

Melanophryniscus stelzneri atroluteus – GALLARDO 1961b.

Melanophryniscus stelzneri montevidensis – KLAPPENBACH 1968b.

Melanophryniscus stelzneri – SKUK 1985.

Melanophryniscus atroluteus – KLAPPENBACH & LANGONE 1992.

Material examined

Brazil (Rio Grande do Sul): Alegrete: UFRGS 2197, Reserva Biologica Ibirapuita, 3/5.XI.2000. – Manoel Viana: ZUFSM 2474, Costa del Rio Ibicuy, 25.X.2000. – São Gabriel: MNHN 1283, Rio Santa María, 10.I.1962. – Uruguaiana: MCN 11470–11471, 25.VI.1977. UFRGS 1771–1772, XI.1997. UFRGS 1810, Termoelétrica AES, 11/15.VII.1997.

Uruguay: **Artigas**: ZVCB 1678, Arrocera Conti, 25.IX.1980. ZVCB 3137, Arrocera Conti, 25 km W de Colonia Palma, 18.X.1982. ZVCB 2313–2320, Arroyo Itacumbú, 24.VII.1977. ZVCB 2500, Arroyo Itacumbú, 1,7 km SE de su boca, 24.VIII.1977. MNHN 1485, Arroyo Itacumbú, Tomás Gomensoro, 10.II.1965. ZVCB 2346, Arroyo Molles del Cuareim, 34 km NW de Artigas, 3.II.1970. MNHN 1484, Arroyo Tres Cruces, 24.XI.1957. ZVCB 2129–2132, Arroyo Yacuí, 5 km arriba Ruta 3, 29.VIII.1978. ZVCB 2421, Bella Unión, XI.1960. ZVCB 3217, Campos RIUSA, 29.VI.1982. ZVCB 2074, Estancia de Washington Carvalho, 11 km W de Colonia Palma, 15.IX.1982. ZVCB 3912, Estancia El Ombú, Río Cuareim, 1.II.1952. ZVCB 254, Región del Yacaré, I.1952. ZVCB 949, Yuquery Orilla próx. Arroyo Molles, 3.II.1970. – **Cerro Largo**: ZVCB 792, 6 km SE de Melo, 22.II.1963. – **Rivera**: ZVCB 10161, Camino de la línea, 10 km NW de la Ciudad de Rivera, 29.X.2001. – **Rocha**: ZVCB 4004–4006, Parque Nacional San Miguel, Cantera Higuerones, 4.V.2000. ZVCB 3888, Ruta 14 km 463, 10.IX.1998. ZVCB 10606–10607, Barra Grande (Laguna de Castillos), 4.X.2003. – **Salto**: ZVCB 1631, El Espinillar, 25/28.X.1979. – **Tacuarembó**: ZVCB 2642–2644, Puntas del Arroyo Cuaró, 26/XI/1993. ZVCB 2789, Puntas del Arroyo Cuaró, 26.XI.1993.

Taxonomic comments

In the original description, MIRANDA-RIBEIRO (1920) suggested that this taxon could be a geographical variation of *M. stelzneri* (Weyenbergh, 1874), and GALLARDO (1961b) treated *M. atroluteus* as a subspecies of *M. stelzneri*. However, GALLARDO (1961b) examined material from "Maldonado", which might actually belong to *M. montevidensis*. CEI (1980) used the name *M. stelzneri montevidensis* to designate populations in Argentina and Uruguay, which are now recognised as *M. atroluteus* (KLAPPENBACH 1969). Based on unpublished morphological features, KLAPPENBACH & LANGONE (1992) elevated *M. atroluteus* to full species rank. This was followed by KWET & MIRANDA (2001), who could partially differentiate between *M. atroluteus* and the nominal form *M. stelzneri stelzneri*, based on bioacoustic data. However, KWET & MIRANDA (2001) suggested that ethological and bioacoustic parameters of *M.*

dorsalis and *M. atroluteus* should be compared. In a recent work, Kwet et al. (2005) did not find significant differences between the advertisement calls of *M. montevidensis* and *M. atroluteus*, and the intraspecific variation in dorsal pattern observed in *M. montevidensis* comprised the pattern variation known for *M. atroluteus*. However, due to the well separated geographical distribution ranges, both taxa were preliminary maintained.

Geographical range

Northeastern Argentina; southern Brazil (northern to centralwestern Rio Grande do Sul); southern Paraguay; Uruguay (eastern, central, northern and northwestern parts).

Conservation status

This species is considered "Not Endangered" in Uruguay and Rio Grande do Sul (Maneyro & Langone 2001; García & Vinciprova 2003). At global level, it is treated as "Least Concern" (IUCN et al. 2006).

Natural history

The habitat of this species (Fig. 11) is associated with rocky soil layers (particularly in Uruguay) and to grassland and open savannas in Brazil (Kwet & Miranda 2001). There are no data available on the diet. Kwet & Miranda (2001) published some details about the reproduction in northern Rio Grande do Sul and mentioned that this species is an explosive breeder, whose reproduction takes place in the summer months during and after heavy rainfall. Recent observations in Rivera department confirmed that explosive breeding takes place in temporary ponds, but reproductive activity was recorded through May, July, August and September (winter months). While in amplexus, males conducted massaging movements with their hind limbs around the cloacal region of the female that, during several dives, released around 100 eggs. An analysis of the call, including sonograms and oscillograms, is found in Kwet et al. (2005). The description of the tadpole is in preparation (D. Baldo pers. comm.), based on specimens from Misiones (Argentina) and Rivera (Uruguay). The characteristic defensive behaviour, termed "Unkenreflex" after the European genus *Bombina*, was reported for *M. atroluteus* by Achaval & Olmos (2003). This behaviour consists of a special body posture including an upward bending of the trunk and demonstration of the red coloured palms and soles to potential predators. We observed this defensive behaviour regularly in specimens collected in Rivera (Uruguay). Analysis of the skin extracts of these toads revealed the presence of many alkaloid compounds, similar to those known for *M. montevidensis* (D. Mebs pers. comm.).

4.1.9 *Melanophryniscus montevidensis* (Philippi, 1902)

Phryniscus nigricans – Duméril & Bibron 1841.
Atelopus montevidensis – Berg 1896.
Phryniscus montevidensis Philippi, 1902. Type: not designated. Type locality: "Montevideo" (Uruguay).
Dendrophryniscus stelzneri – Müller & Hellmich 1936.
Melanophryniscus stelzneri atroluteus – Gallardo 1961b.
Melanophryniscus stelzneri – Vaz Ferreira et al. 1966.
Melanophryniscus stelzneri montevidensis – Klappenbach 1968b.
Melanophryniscus montevidensis – Klappenbach & Langone 1992.

Material examined

Brazil (Rio Grande do Sul): Santa Vitória do Palmar: ZVCB 7276–7278, Alvorada, II.1989. UFRGS 1845–1847, Fazenda Portão de Ferro (Lag. Mangueira), 15.XII.1999.

Uruguay: **Rocha**: ZVCB 3453, 1 km E de La Pedrera, I.1998. MNHN 6688, Aguas Dulces, 28.XII.1998. MNHN 1152, Arroyo San Miguel, XI.1962. ZVCB 4858–4860, Balneario Perla de Rocha, km 258 Ruta 10, 5.I.1998. ZVCB 10481–10501 and 10506–10509, Barra de la Laguna de Rocha, 24.VIII.2002. ZVCB 10615–10639, Barra de la Laguna de Rocha, 25.X.2003. MNHN 6681, Barra del Arroyo Valizas, 1.I.1988. ZVCB 203, Barra del Chuy, 22.I.1962. MNHN 699, Cabo Polonio, I.1959. ZVCB 30, Cabo Polonio, III.1955. ZVCB 32, Cabo Polonio, III.1955. ZVCB 72, Cabo Polonio, VII.1951. ZVCB 256, Cabo Polonio, 13.X.1953. ZVCB 473, Cabo Polonio, 11.III.1956. ZVCB 497, Cabo Polonio, I.1966. ZVCB 624, Cabo Polonio, 8.VII.1960. ZVCB 638, Cabo Polonio, II.1945. ZVCB 1064, Cabo Polonio, II.1960. ZVCB 1515, Cabo Polonio, II.1977. ZVCB 1552, Cabo Polonio, 2.II.1977. ZVCB 1660, Cabo Polonio, 11.II.1980. ZVCB 1664, Cabo Polonio, 7.II.1980. ZVCB 1788, Cabo Polonio, 14.II.1980. ZVCB 1800–1801, Cabo Polonio, 11.I.1981. ZVCB 1894–1950, Cabo Polonio, 18.II.1971. ZVCB 2241–2245, Cabo Polonio, 9.II.1978. ZVCB 2422–2423, Cabo Polonio, I.1966. ZVCB 2720–2721 and 2741–2744, Cabo Polonio, 12.IV.1995. ZVCB 3904, Cabo Polonio, 13.III.1953. ZVCB 4026, Cabo Polonio, 1.II.1971. ZVCB 10340–10343, Cabo Polonio, 26/27.II.2003. ZVCB 10505, Cabo Polonio, 20.II.2003. ZVCB 490, Cabo Polonio, Zona de Valizas, III.1943. MNHN 398, Castillos, 12.XI.1956. ZVCB 856 and 918, Charco al lado del Arroyo Valizas, 9.III.1959. MNHN 6682, Chuy, 24.III.1984. ZVCB 1703–1705, Coronilla, 3.I.1981. ZVCB 4832–4835, Entrada a Aguas Dulces (Ruta 16), 1.I.1998. MNHN 6680, La Coronilla, 1986. MNHN 2478, La Paloma, 3.I.1973. MNHN 4898, La Paloma, 1.I.1955. ZVCB 1147–1149, La Paloma, 7.III.1966. ZVCB 1180, La Paloma. ZVCB 1892, La Paloma, 18.IV.1980. ZVCB 1283, La Pedrera, 6.I.1975. SMNS 11807–11816, Laguna de Rocha, 24.X.2003. ZVCB 3942–3945, Laguna de Rocha, 8.XII.1999. ZVCB 10571, Laguna de Rocha, 11.IX.2003. ZVCB 10914–10915, Oceanía del Polonio, 18/20.IX.2002. ZVCB 346, Parque Nacional Santa Teresa, 28.II.1965. ZVCB 10481–10501, Parque Nacional Lacustre, Laguna de Rocha, 24.VIII.2002. ZVCB 10432–10443, Perla de Rocha, 20.I.2004. MNHN 3115, Playa Arachania, 3.X.1982. ZVCB 8289–8291, Playa Sur (Cabo Polonio), 12.I.2001. MNHN 2123, Punta del Diablo, 3.XII.1973. ZVCB 4848–4849, Punta Rubia, 23.IX.2000. MNHN 2391, Santa Teresa, 20.I.1973. ZVCB 1432, Santa Teresa, 26.I.1948. ZVCB 3293–3304, Vivero Día Forestal, Ruta 10, Cabo Polonio, 5.X.1985.

Taxonomic comments

Melanophryniscus montevidensis was originally described as a species of *Phryniscus*, but this genus name is

not valid because it is based upon a specimen of *Bufo spinulosus* (see GALLARDO 1961b). Subsequently the species was assigned to the genera *Atelopus* and *Dendrophryniscus* (BERG 1896; CORDERO 1919; NIEDEN 1926; MÜLLER & HELLMICH 1936) and, after the description of *Melanophryniscus* by GALLARDO (1961c), it was placed in this genus. However, GALLARDO (1961b) considered *montevidensis* a subspecies of *M. stelzneri*. See comments on *M. atroluteus* in GALLARDO (1961b) and KLAPPENBACH & LANGONE (1992), who elevated the taxon to specific rank. KWET et al. (2005) provided a bioacoustic analysis and maintained the validity of *M. montevidensis*, despite the similarity to the call of *M. dorsalis*.

Geographical range

Rio de la Plata shoreline and Atlantic coast in Uruguay. To date, the only record from Brazil (TEDROS et al. 2001) is from Alvorada (Barra do Chui) in the extreme south of Rio Grande do Sul.

Conservation status

Uruguayan populations are considered "Endangered" (MANEYRO & LANGONE 2001). One of the presumable causes for the observed populational declines is assigned to the urbanisation process along the Uruguayan coast (LANGONE 1995). Although the species is not included in the red list of Rio Grande do Sul (GARCÍA & VINCIPROVA 2003), its restricted geographical occurrence in this state may justify the inclusion as an endangered species. At global level it is treated as "Vulnerable" (IUCN et al. 2006).

Natural history

This species is only known from sandy environments (Fig. 12), like coastal dunes near the Rio de la Plata and Atlantic Ocean (LANGONE 1995). There is little information on its diet, but KOLENC (1987) and LANGONE (1995) listed ants, mites, small beetles, collembolans and aphids as main prey items. Recent data from faeces revealed that these toads fed mainly on ants (i.e. genus *Pheidole*) and mites (MEBS et al. 2005). The advertisement call (sonograms and oscillograms) was described by KWET et al. (2005), and the complex reproductive behaviour including cloacal massages from male to female was described by ALONZO et al. (2002). The egg oviposition occurring in several dives was described by KLAPPENBACH (1969) and PRIGIONI & GARRIDO (1989). *Melanophryniscus montevidensis* is an explosive breeder and its reproductive activity seems to correspond with heavy rainfall during warm days (LANGONE 1995; MANEYRO et al. 1995). The tadpole was described by GARRIDO-YRIGARAY (1989), and there is a reference to albino larvae in a population from Rocha department (MANEYRO & ACHAVAL 2004). As in the case of *M. atroluteus*, this species exhibits a defensive behaviour named "Unkenreflex" (LANGONE 1995). In the skin of these toads, several toxic compounds were found like pumiliotoxins (an alkaloid described from Dendrobatidae and Mantellidae) and hydroquinones (MEBS et al. 2005).

4.1.10 *Melanophryniscus* sp.

Melanophryniscus sp. MANEYRO et al., in press. Designated holotype: ZVCB 5334. Type locality: "Establecimiento Trinidad (30°53'S, 55°33'W), approximately 230 m elevation, Rivera department, Uruguay".

Material examined

Uruguay: **Rivera**: ZVCB 5334, Est. Trinidad, 23.III.2001 (holotype). ZVCB 6375, Est. Vázquez, 12.V.2001 (paratype). ZVCB 8129, Est. Vázquez, 7.VII.2001 (paratype). ZVCB 8336, Est. Trinidad, 14.IX.2001 (paratype). ZVCB 9389, Est. Trinidad, 12.I.2002 (paratype).

Taxonomic comments

This species is placed in the *M. moreirae* species group according to the original description (MANEYRO et al. in press).

Geographical range

Currently, this species is only known from the type locality and surrounding areas in northern Rivera department. However, the vicinity of these localities to the Brazilian border makes its presence in Rio Grande do Sul possible.

Conservation status

This species is not yet evaluated, neither at global nor regional levels. However, the presumed restricted distribution range in a highly modified environment suggests that this taxon should be placed in one of the threat categories.

Natural history

The habitat of this species is situated in the low hill region in northern Uruguay (Fig. 13), actually modified by plantations with *Eucalyptus* sp. and *Pinus* sp. (MANEYRO et al. in press). Nothing is known about the diet, and also the tadpole and advertisement call of this toad remain unknown. Based on indirect evidence, the reproductive period seems to be in the winter months.

4.1.11 *Melanophryniscus sanmartini* Klappenbach, 1968

Melanophryniscus sanmartini KLAPPENBACH, 1968b. Holotype: MNHN 1676. Type locality: "Villa Serrana, próximo a la represa del arroyo Aiguá, departamento de Lavalleja, República del Uruguay" (Villa Serrana, close to the dam of Aigua River, Lavalleja department, Uruguay).

Material examined

Uruguay: **Rivera**: ZVCB 6376–6377, Est. Rocha, 8/11.IV.

2001. ZVCB 8132, Est. Rocha, 7/9.VII.2001. ZVCB 8206, Est. Rocha, 10/13.VIII.2001. ZVCB 9390, Est. Rocha, 10/12.XI.2001. ZVCB 6371–6372, Est. Trinidad, 8/11.IV.2001. ZVCB 8077, Est. Trinidad, 9/11.VI.2001. ZVCB 8639–8657 and 8727–8731, Est. Trinidad, 10/12.XI.2001. ZVCB 8817, 8852–8857 and 8904–8907, Est. Trinidad, 10/11.XII.2001. ZVCB 8981, Est. Trinidad, 12/14.I.2002. ZVCB 6373–6374, Est. Vázquez, 8/11.IV.2001. ZVCB 8189–8190, Est. Vázquez, 10/13.VIII.2001. ZVCB 8358, Est. Vázquez, 14/16.IX.2001. – **Rocha**: MNHN 1154, Parque Nacional San Miguel, 21.IX.1962.

Taxonomic comments

This species was placed in the *M. moreirae* group by Caramaschi & Cruz (2002), Cruz & Caramaschi (2003) and Larson et al. (2003). The specimen MNHN 0392, in the original description designated paratype, corresponds to *M. orejasmirandai* (see Prigioni & Langone 1986).

Geographical range

The species is only known from a few localities in southern and central Uruguay. However, some allopatric populations were recently reported from Rivera department nearby the Brazilian border (Naya & Maneyro 2001) and its presence in Rio Grande do Sul seems highly probable.

Conservation status

Melanophryniscus sanmartini was considered "Endangered" in Uruguay by Maneyro & Langone (2001). Although this rare species is endemic in Uruguay, it is considered as "Near Threatened" by IUCN et al. (2006).

Natural history

This species occurs in low hill landscapes until 350 m a. s. l. (Fig. 14). Adult specimens were found in modified habitats in Rivera department, i. e. in artificial forests (Naya & Maneyro 2001). There are no data available on the diet of this species. Achaval & Olmos (2003) indicated that its reproductive activity may occur from April to November after heavy rainfall, but probably this species reproduces during the whole year. The tadpole was described by Prigioni & Arrieta (1992). In an unpublished congress abstract, the advertisement call was described as a succession of short trills (Borteiro et al. 2006b).

4.1.12 *Melanophryniscus devincenzii* Klappenbach, 1968

Melanophryniscus devincenzii Klappenbach, 1968b. Holotype: MNHN 1675. Type locality: "La Palma, Rubio Chico, próximo a la Subida de Pena, Cuchilla Negra, departamento de Rivera, República del Uruguay" (La Palma town, Rubio Chico stream, close to Pena climbing, Cuchilla Negra, Rivera department, Uruguay).

Material examined

Uruguay: **Rivera**: SMNS 11829, Arroyo Rubio Chico, 20/22.X.2003. ZVCB 10661 and 10855, Arroyo Rubio Chico (Ruta 30), 20/22.X.2003. ZVCB 10614, Est. Los Abuelos, Campos de FYMSA, 16.VIII.2003. MNHN 1675, La Palma, Rubio Chico, Cerca de subida de Pena, 11.IV.1968 (holotype). – **Tacuarembó**: MNHN 1471, Gajo Norte del Arroyo Tres Cruces (Sierras del Infiernillo), 12.II.1963 (paratype). MNHN 1673, Puntas del Arroyo Laureles, 12.XII.1965 (paratype).

Taxonomic comments

The species was placed in the *M. tumifrons* group by Caramaschi & Cruz (2002), Cruz & Caramaschi (2003) and Larson et al. (2003). The allopatric Argentinean populations cited by Baldo & Krauczuk (1999) might belong to another, yet undescribed taxon.

Geographical range

To date, this species is only known from some localities in northern Uruguay (departments of Tacuarembó and Rivera). Di-bernardo et al. (2004) stated for this species a "possible occurrence" in Candiota municipality (Rio Grande do Sul), perhaps following Céspedez & Motte (2001), but the latter authors did not provide collection numbers of voucher specimens and their citation might be erroneous. However, the occurrence of *Melanophryniscus devincenzii* is confirmed from some Uruguayan localities nearby the borderline (i. e. Cuchilla Negra, Rivera department) and actually the species' presence in Brazil seems highly probable.

Conservation status

This species is considered "Endangered" in Uruguay (Maneyro & Langone 2001) and at global level (IUCN et al. 2006).

Natural history

The habitat of this taxon lies in the low hill region in northern Uruguay (Fig. 15). There are no data published on its diet, but the main items in faeces from specimens collected at Cuchilla Negra (Rivera department) were ants. *Melanophryniscus devincenzii* was observed in reproductive activity during winter and spring after heavy rainfalls in small ephemeral streams on the top of a hill at Cuchilla Negra. Males vocalised during the day until sunset; several pairs in axilar amplexus were observed at the stream margin, out of the water. At the same locality, many interspecific amplectant pairs between *M. devincenzii* (males) and *M. atroluteus* (females) could be observed, and one of the males looked like a hybrid between both species. The advertisement call of *M. devincenzii* was similar that of other species in the *M. stelzneri* group, although the second part of the call (vibration) was longer. The vocalisation of the mentioned hybrid male had an intermediate duration (shorter than in *M. devincenzii*, but longer than in *M. atroluteus*). Tadpoles were found in the

backwater of the streams; a brief description of these larvae is given in KOLENC et al. (2003).

4.1.13 *Melanophryniscus pachyrhynus* (Miranda-Ribeiro, 1920)

Atelopus pachyrhynus MIRANDA-RIBEIRO, 1920. Types: MZUSP 752 (two specimens) and MZUSP 756; the latter was designated lectotype by CARAMASCHI & CRUZ (2002). Type locality: "Rio Grande do Sul ... São Lourenço, S. Paulo", Brazil; corrected as "São Lourenço in Rio Grande do Sul" by BOKERMANN (1966) and restricted as "Brazil, Rio Grande do Sul, São Lourenço do Sul (31°22'S, 51°59'W)" by CARAMASCHI & CRUZ (2002).

Melanophryniscus pachyrhynus – CARAMASCHI & CRUZ 2002.

Material examined

Uruguay: **Cerro Largo**: ZVCB 11097–11098, Sierra de Mangrullo (Río Yaguarón), 16.V.2004.

Taxonomic comments

Shortly after its description, this species was placed in the synonymy of *M. tumifrons* by MÜLLER (1934), which was followed by most subsequent authors (e. g. CEI 1980). However, PRIGIONI & LANGONE (1986) suggested the possible validity of *M. pachyrhynus*, and CARAMASCHI & CRUZ (2002) removed this taxon from the synonymy placing it to the *tumifrons* group.

Geographical range

This species known only from its type locality in São Lourenço, was recently also collected in São Jerônimo, Rio Grande do Sul (R. BALLESTRIN pers. comm.), and Cerro Largo department, Uruguay (KOLENC et al. 2005).

Conservation status

At global level this species is considered "Data Deficient", because of the absence of recent data on distribution, abundance and ecological requirements (IUCN et al. 2006). It was not evaluated for neither Rio Grande do Sul (GARCÍA & VINCIPROVA 2003) nor Uruguay (MANEYRO & LANGONE 2001).

Natural history

This species occurs in the low hill regions of northeastern Uruguay and the Serra de Sudeste in Rio Grande do Sul (Fig. 16). Nearly nothing is known about its biology. A brief description of the tadpole was recently presented as unpublished congress abstract (KOLENC et al. 2005).

4.2 Key to the species of Bufonidae in the border region Uruguay/Brazil

1 Presence of parotoid glands. . . . . (genus *Chaunus*). **2**
– Absence of parotoid glands. . . (genus *Melanophryniscus*). **8**
2 Presence of tarsal folds. . . . . (*Chaunus marinus* group). **3**
– Absence of tarsal folds. **6**
3 Presence of distinct tibial glands. . . ***C. schneideri*** (Fig. 22)
– Absence of tibial glands. **4**
4 Shape of parotoid glands subtriangular, posterior portion of these glands continuing as a longitudinal glandular string. . . . . ***C. arenarum*** (Fig. 20)
– Shape of parotoid glands rounded or ovoid and posterior portion of these glands truncated, without a longitudinal glandular string. **5**
5 Toes long (second toe's length 1.5 times diameter of outer metacarpal tubercle). Parotoid glands elongated (more than twice as long as broad). . . . . ***C. achavali*** (Fig. 19)
– Toes shorter. Parotoid glands not elongated (longitudinal diameter less than twice transversal diameter). . . . . ***C. ictericus*** (Fig. 21)
6 Snout sloping in lateral view (maxilla larger than mandible). Parotoid glands large to medium-sized. . . . . (*Chaunus crucifer* group). ***C. henseli*** (Fig. 23)
– Snout vertical in lateral view (maxilla length equal to mandible length). Parotoid glands small. . . . . (*Chaunus granulosus* group). **7**
7 Supraocular crests well developed. Subocular crests absent (if present, poorly developed and never reaching postocular crests). . . . . ***C. dorbignyi*** (Fig. 17)
– Supraocular crests weakly developed. Subocular crests present (generally ultrapassing postocular crests). . . . . ***C. fernandezae*** (Fig. 18)
8 Presence of frontal swelling. . . . . (*Melanophryniscus tumifrons* group). **9**
– Absence of frontal swelling. **10**
9 Belly and chest light coloured (orange in living animals), splashed with black spots. . . . . ***M. pachyrhynus*** (Fig. 27)
– Belly black with a light subtriangular spot (red in living specimens). . . . . ***M. devincenzii*** (Fig. 26)
10 Dorsal colouration dark brown. . . . . (*Melanophryniscus moreirae* group). **11**
– Dorsal colouration black. . . . . (*Melanophryniscus stelzneri* group). **12**
11 Dorsal skin with longitudinal glandular ridges, gular region uniformly black, without spots or blotches. . . . ***M.*** sp. (Fig. 24)
– Dorsal skin presenting rounded glandular warts, gular region black with an ocher blotch just near tip. . . . . ***M. sanmartini*** (Fig. 25)
12 Dorsal surface uniformly black, never presenting pale blotches; skin generally strongly granulated. . . . . ***M. atroluteus*** (Fig. 28)
– Dorsal surface black, usually with pale (yellow in living specimens) lateral blotches (sometimes absent); skin weakly granulated. . . . . ***M. montevidensis*** (Fig. 29)

4.3 Zoogeographical considerations

Several hypotheses are discussed regarding possible zoogeographical processes that determine the distribution patterns of amphibians in the border region between Uruguay and Brazil. Some of these patterns are historically funded and based upon biological similarities among species. One of the first faunistic groups was suggested for amphibians associated with the Chaco region (VELLARD 1948). The chacoan group includes species with special adaptations to periodical desiccation. Among bufonids, *C. schneideri* is a typical species inhabiting the chacoan region. GALLARDO (1964) characterised a second group as litoral-mesopotamic amphibian fauna, combining chacoan

species with species occurring in the basins of the Uruguay and Paraná rivers. This group was also recognised by LUTZ (1967), who assigned the species to the transitional fauna between the Chaco and the arid Pampas region, as proposed by CEI (1953). GALLARDO (1974b) suggested three main speciation centers for South American amphibians, i.e. holarctic, Andino-Patagonic and Guayano-Brazilian (GALLARDO 1974b, 1979). The species in the border area are included in the Guayano-Brazilian group. Additionally, dispersion along large hydrographic basins and the theory of refuges were proposed as possible speciation mechanisms for some species, such as for the taxa in the *Chaunus granulosus* group (GALLARDO 1969; 1979).

Although the chacoan and litoral-mesopotamic amphibian fauna may have a Guayano-Brazilian origin, both are enriched by endemic species and impoverished by climatic factors (GALLARDO 1966). Because there are no physical barriers between these zoogeographical regions, chacoan species could have entered the litoral-mesopotamic region and, conversely, some litoral-mesopotamic anurans may have adapted to chacoan conditions. Based on previous studies (VELLARD 1948; CEI 1950; GALLARDO 1964), parallelisms between chacoan and litoral-mesopotamic species were hypothesised by GALLARDO (1966), who suggested that, among other species pairs, the ecological equivalents of the chacoan bufonids *C. schneideri* and *C. major* are the litoral-mesopotamic *C. arenarum* and *C. fernandezae*.

The amphibian fauna of central Argentina (Buenos Aires and La Pampa provinces) shows many similarities in species composition with the fauna of Uruguay and Rio Grande do Sul, e.g. many species belong to Leptodactylidae, Leiuperidae, Ceratophryidae, and Bufonidae (GALLARDO 1965d; MANEYRO et al. 1995). Among these amphibians a particular group has been characterised as Atlantic shore fauna (MANEYRO et al. 1995; MANEYRO & CARREIRA 2006) containing *Chaunus arenarum*, *Melanophryniscus montevidensis* and *Ceratophrys ornata*. Other species, which are associated with superficial soils, an environment typical for the low hill regions of northern Uruguay, has been designated as riograndense fauna (MANEYRO et al. 1995), e.g. *Limnomedusa macroglossa*, *Phyllomedusa iheringii*, *Physalaemus cuvieri*, *P. riograndensis* and *Melanophryniscus atroluteus* (MANEYRO & BEHEREGARAY in press). These species may be related to the Misiones fauna, which was described by GALLARDO (1961a) and later confirmed by LUTZ (1967) and GALLARDO (1986). LUTZ (1967) also suggested that many species inhabiting flooded grassland in the litoral mesopotamic region are also found in the hill regions of Misiones and Rio Grande do Sul meaning altitude may compensate the latitudinal effect.

Based on this theoretical frame work, the bufonid fauna occurring in the border region between Uruguay and Brazil can be zoogeographically classified in five major groups: (1) species associated with the dune region on the Atlantic shore (*C. arenarum* and *M. montevidensis*); (2) toads of the *Chaunus granulosus* group (*C. dorbignyi* and *C. fernandezae*), which are associated with the Argentinean litoral-mesopotamic fauna; (3) species characteristic for the chacoan region occurring close to the Uruguay River (*C. schneideri*); (4) the most speciose group with toads inhabiting the low hill region, composed by *C. achavali*, *M. atroluteus*, *M. devincenzii*, *M. pachyrhynus*, *M. sanmartini*, and *M.* sp.; (5) the two remaining species, *C. ictericus* and *C. henseli*, which are not characteristic for the border region, being associated with the Atlantic forest biome and distributed further to the north.

Many questions remain about the Bufonidae in this area. Among the species in the *Chaunus granulosus* group, two taxa are currently recognised, *C. dorbignyi* and *C. fernandezae*. The former should inhabit the southeastern range, whereas the latter is more frequent in the northwestern part. However, there are many specimens exhibiting intermediate phenotypes and their assignment to one of both taxa is difficult or even impossible. This agrees with NARVAES (2003), who concluded that overlapping distribution ranges in *C. dorbignyi* and *C. fernandezae* mean that these toads could regularly hybridise in nature. Among the amphibians occurring in the border region between Uruguay and Brazil, many species are of particular interest, especially those with small distribution areas or putative endemic species as *M. devincenzii* and *C. achavali*. These taxa which are generally considered as "Endangered" (MANEYRO & LANGONE 2001; MANEYRO et al. 2004) inhabit predominantly environments with soils classified as "prioritary for forestation". Severe modifications in these landscapes are expected in the next years, and undoubtedly taxon specific studies quantifying the impact of such activities on amphibian populations will be necessary for developing successful conservation policies.

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Note added in proof: CHAPARRO et al. (2007) placed the generic name *Chaunus* into the synonymy of *Rhinella* and suggested to use *Rhinella dorbignyi*, *R. fernandezae*, *R. achavali*, *R. arenarum*, *R. icterica*, *R. schneideri*, and *R. henseli*.

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Manuscript received: 7.III.2007, accepted: 5.VII.2007.

Notes on the *Praomys* of Angola with the description of a new species (Mammalia: Rodentia: Muridae)

Erik Van der Straeten

Abstract

A new species of the *Praomys tullbergi* species-complex, *P. coetzeei* **n. sp.**, is described and compared with the other species of this complex. In the northeast of Angola the species of the *P. tullbergi* complex and the *P. jacksoni* complex have a sympatric distribution.

Keywords: *Praomys*, Angola, new species.

Zusammenfassung

Eine neue Art aus der *P. tullbergi* Arten-Gruppe, *P. coetzeei* **n. sp.**, wird beschrieben und mit den Arten dieser Gruppe verglichen. In Nordost-Angola zeigen die Arten der *P. tullbergi*-Gruppe und der *P. jacksoni*-Gruppe eine sympatrische Verbreitung.

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1 Introduction

Van der Straeten & Dudu (1990) recognized four different species-complexes within the genus *Praomys*: the *P. jacksoni* group, the *P. tullbergi* group, the *P. delectorum* group, and the *P. lukolelae* group. In other publications I discussed the differences between these four species-complexes, with special emphasis on the *P. tullbergi* group (Van der Straeten & Verheyen 1981; Van der Straeten & Dieterlen 1987; Van der Straeten & Dudu 1990; Van der Straeten et al. 2003).

Only a few publications mention the presence of *Praomys* in Angola. Specimens of this genus were not recorded by Hill & Carter (1941). Sanborn (1952) was the first to locate *Praomys jacksoni jacksoni* in the Lunda District. This was confirmed by Hayman (1963) who identified his specimens as *Rattus (Praomys) morio jacksoni*. Musser & Carleton (1993) were the first to mention a second species, *Praomys tullbergi*, in the north of Angola. They claim that the distribution limits of *Praomys tullbergi* are unknown.

Crawford-Cabral (1998) gives an overview of the distribution of all Muroidea in Angola. His information is based on literature and specimens housed in museums in Lisboa and Angola and in the FMNH. He thinks that it is possible that *Praomys tullbergi* and *P. jacksoni* have allopatric distributions in Angola, respectively in the northwest and the northeast of this country.

During a stay in different museums I had the opportunity to study two interesting collections from the north of Angola: the specimens collected by Heinrich in 1954 (stored in FMNH), and the collection made by Feiler in 1983 (stored in SNSD). While studying the specimens, it was clear for me that the '*tullbergi*' specimens are a big representative of the *P. tullbergi* species-complex, related to *P. rostratus* and *P. petteri*. Further studies and biometrical analyses demonstrated that these specimens belong to a new species.

Acknowledgments

I am grateful to the following colleagues for allowing me to examine specimens under their care: D. Schlitter (CM), W. Stanley (FMNH), W. Van Neer (KMMA), L. de Roguin (MHNG), M. Tranier and J. Cuisin (MNHN), J. Ingles and P. Jenkins (NHM), F. Dieterlen (SMNS), T. Ziegler (SNSD), R. Hutterer (ZFMK), and A. Dudu (private collection). I am also indebted to R. Hutterer and F. Dieterlen for the review of the manuscript. My special thanks are due to R. Banasiak (FMNH), W. Stanley and R. Hutterer for providing the photos of the new species, and to P. Yde (Antwerpen) for carefully checking the English text.

The fieldwork in Cameroun and the stay of the author in different museums was funded by the Belgian National Foundation for Scientific Research (Fonds voor Wetenschappelijk Onderzoek).

2 Material and methods

For this study I examined *Praomys* specimens from the following museums, institutions and private collections:

CM	Carnegie Museum of Natural History, Pittsburgh
DUD	Collection A. Dudu, Kisangani (République Démocratique du Congo)
FMNH	Field Museum of Natural History, Chicago
KMMA	Koninklijk Museum voor Midden Afrika, Tervuren
MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
NHM	The Natural History Museum, London
RUCA	Departement Biologie, Universiteit Antwerpen
SMNS	Staatliches Museum für Naturkunde, Stuttgart
SNSD	Staatliche Naturhistorische Sammlungen, Dresden
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn

The following specimens were used:

Praomys coetzeei n. sp.

See list of type material in chapter 3.

Praomys cf. *jacksoni* de Winton, 1897

Angola: Dundo (NHM 63.1089–1092); Duque de Bragança (25 km N – 15 km E) (FMNH 81983–85, 81990–92, 82005); Luhanda (FMNH 82011, 81924); Uige (SNSD B14139–41).

Praomys misonnei Van der Straeten & Dieterlen, 1987

République Démocratique du Congo: Batiabongena (DUD 69, 95, 305, 379, 431, 440, 513, 515, 532, 544, 545, 615, 1052, 1804, 1861, 2216, 2225, 2556, 2561, 2584, 2596, 3088, 4354, 4355, 4390); Irangi (SMNS 10460, 10494, 10504–505, 10507, 10511, 10518, 10549, 10552, 10554, 10555 holotype, 10562, 10565, 10595, 10601, 10609, 10613, 10617, 10621, 10623, 10631, 10632, 10647, 10650, 10659, 10670, 20449, 20511, 20526, 20537, 20541, 20570, 20621).

Praomys petteri Van der Straeten, Lecompte & Denys, 2003

République Centrafricaine: Boukoko (MNHN 1963/587, 1963/592, 1963/1093, 1967/1557, 1967/1576, 1967/1581, 1971/518 holotype, 1971/519, 1979/113; ZFMK 70.146–47, 92.319–22); Ngueguey (MHNG 1686.51–53). – **Cameroun**: Metet (CM 4647); Mieri-Bimba (RUCA 2956/0/19, 0/27/10); Nkolbisson (MNHN 1970/326); Yaoundé (MNHN 1969/111, 1975/430–431); Yokadouma (MNHN 1952/445, 1952/448); Zoatoupsi (MNHN 1983/32–33); locality unknown (RUCA 2.867). – **Congo**: Béna (MNHN 1991/105–108); Kuilela (MNHN 1991/431–437, 1991/439–442); M'Bila (MNHN 1965/70); Ménengué (MNHN 1991/109); Tchissanga (MNHN 1991/104, 1991/110–113, 1991/115); locality unknown (MNHN 1991/1110).

Praomys tullbergi Thomas, 1894

Côte d'Ivoire: Adiopodoumé (KMMA 80.009M0002, 80.009M0003, 80.009M0005, 80.009M0006, 80.009M0008, 80.009M0010, 80.009M0011, 80.009M0013, 80.009M0018, 80.009M0019, 80.009M0021–80.009M0025, 80.009M0028, 80.009M0030, 80.009M0032, 80.009M0033, 80.009M0035–80.009M0038, 80.009M0040, 80.009M0047, 80.009M0052, 80.009M0055, 80.009M0063, 80.009M0067, 80.009M0068, 80.009M0070); Lac Lallié (KMMA 989); Lamto (KMMA 1268, 1342).

The other species of the *Praomys tullbergi* complex were not included in this study. *P. morio* Trouessart, 1881 is closely related to *P. tullbergi* but has a very restricted distribution: it is only found on Mount Cameroun above 1000 m and on higher parts (above 1200 m) of Bioko. A biometrical comparison of *P. morio* and *P. tullbergi* indicates that they can be considered as two different species. *P. rostratus* is only found in West-Africa, west of the Dahomey Gap. Also *P. hartwigi* Eisentraut, 1968 and *P. obscurus* Hutterer & Dieterlen, 1992 were not used for this study since they also have a very restricted distribution; they are only known from Mount Oku in Cameroun and Gotel Mountains in Nigeria.

Statistical methods, definitions and descriptions of measurements (see Tab. 1) follow Van der Straeten & Van der Straeten-Harrie (1977) and Van der Straeten & Dieterlen (1987). For the canonical analysis (Seal 1964) I used the method, terminology and programs adapted by Hebrant (1974). This analysis maximizes the between groups variation in relation to the within groups variation. The original variables are transformed to a new set of canonical variables. Thereto eigenvalues and eigenvectors are calculated. This permits representation of the specimens and of the group centroids. For a specimen each original variable (measurement) is multiplied by its corresponding coefficient of the eigenvector and the obtained values are added up. This must be done for all specimens in each of the canonical variates. Now, using the obtained values, each specimen can be plotted in a diagram of canonical variates represented as an abscissa or an ordinate. Neighbouring groups are biometrically more related than distant ones (Van der Straeten & Dieterlen 1987). External body measurements were recorded from specimen labels. Specimens were divided into arbitrary age groups using the degree of wear on the first and second upper molars (Verheyen & Bracke 1966). These age groups were tested to evaluate their statistical integrity.

3 Description of *Praomys coetzeei* n. sp.

Holotype: Adult male (age class 5), skin and skull, FMNH 81981 [original number 8217], Angola, Duque de Bragança (25 km N – 15 km E), collected by G. Heinrich, 26.V.1954.

Paratypes (listed as follows: locality, total number in parentheses, sex and specimen number associated with museum acronym): Angola (17): same data as holotype (6), male FMNH 81989, 81993, 82002, 82004, female FMNH 81994, 82003; Gabela, 30 km S (1) male FMNH 83843; Luhanda (4) male FMNH 82006, 82013, female FMNH 82012, 82015; Sanza Pombo (1) SNSD B14135; Uige (5) male SNSD B14130–32, female SNSD B14133, B14136.

Etymology

I name this new species of *Praomys* in honour of my friend and colleague Neels Coetzee to express my appreciation for his contributions to the knowledge of the mammal fauna in southern Africa.

Diagnosis

Praomys coetzeei n. sp. has the typical characters of the *P. tullbergi* species-complex. It is one of the large members of this complex and is related to *P. rostratus* and *P. petteri*. Compared with *P. petteri*, the rostrum of *P. coetzeei* is shorter and less high. *P. coetzeei* has a long foot of 24–28 mm, the same as in *P. petteri*; in *P. tullbergi* the length of the foot is 23–26 mm, in *P. misonnei* 21.0–25.5 mm and in *P. rostratus* 25–29 mm.

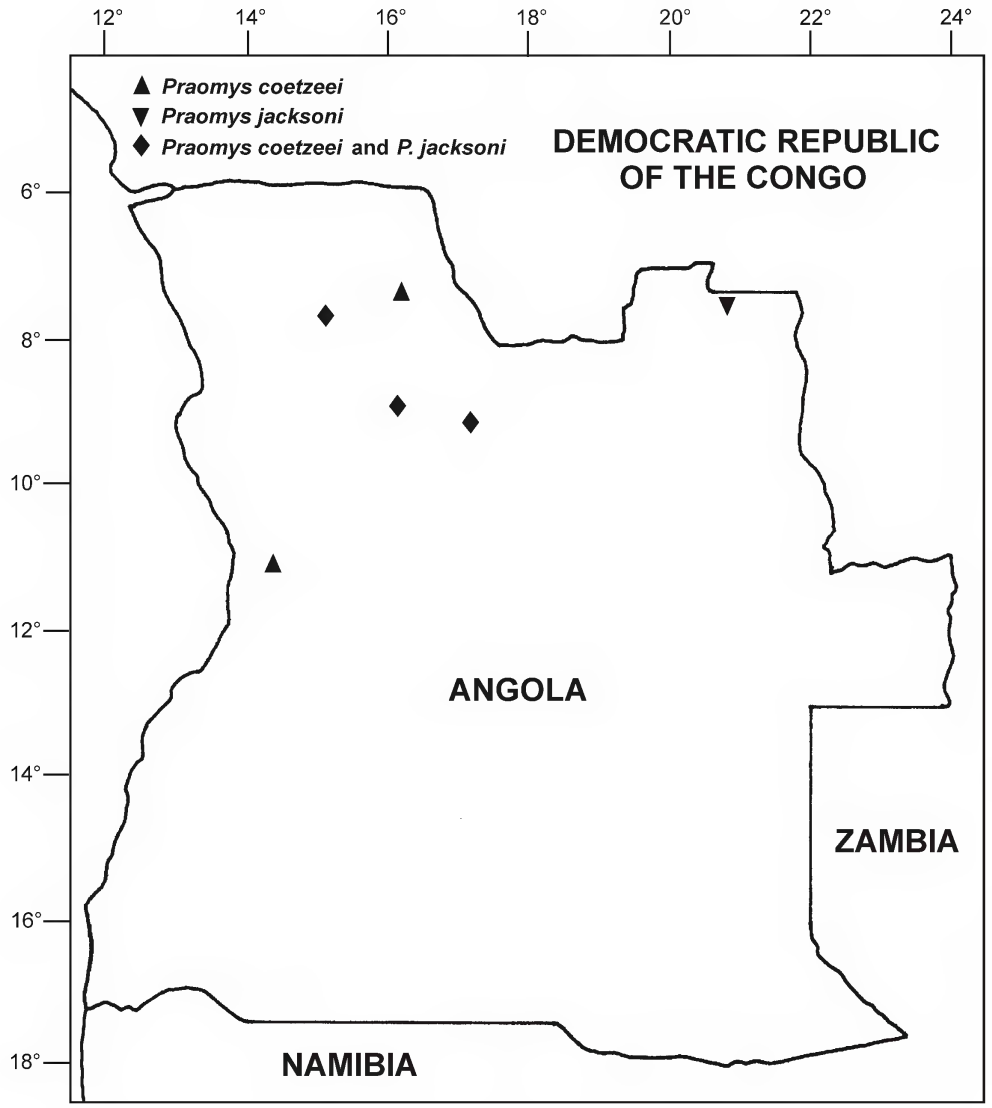

Fig. 1. Distribution of *Praomys coetzeei* n. sp. and *P.* cf. *jacksoni* in Angola (specimens housed in FMNH, NHM and SNSD).

P. coetzeei can easily be characterized by a canonical analysis using skull measurements (Figs. 3, 4).

Distribution

This species is known only from the northwest of Angola. In this region it occurs sympatrically with *Praomys* cf. *jacksoni* (Fig. 1). However, I do not exclude that it is also present in the northeast of Angola. Only a throughout study of specimens in the Instituto Superior de Ciências da Educação, Lubango and the Museo do Dundo, both in Angola, can solve this problem.

Following the museum labels specimens were captured in primary wood, secondary wood, gallery wood and a tropical wood stripe along a river.

Description

P. coetzeei has all the characteristics of the *P. tullbergi* species-complex. The t^3 on M^1 is obsolete or difficult to detect; very few specimens have a trace of a t^3 on M^1. On M^2 the t^3 is small or very small; t^3 is absent in M^3. The t^9 is clearly present in M^1 and M^2 Mostly the t^7 is present as a faint ridge in M^1 and M^2. The supra-orbital ridges are weak and not at all raised (but angular in older specimens) and the interorbital constriction is smooth and has a slightly amphoral pattern. The anterior palatal foramina reach up to the front edge of the first root of M^1. Skull see Fig. 2.

The pelage is soft and without underfur. The colour of the dorsal pelage is brown, slightly darker than in *P. tull-*

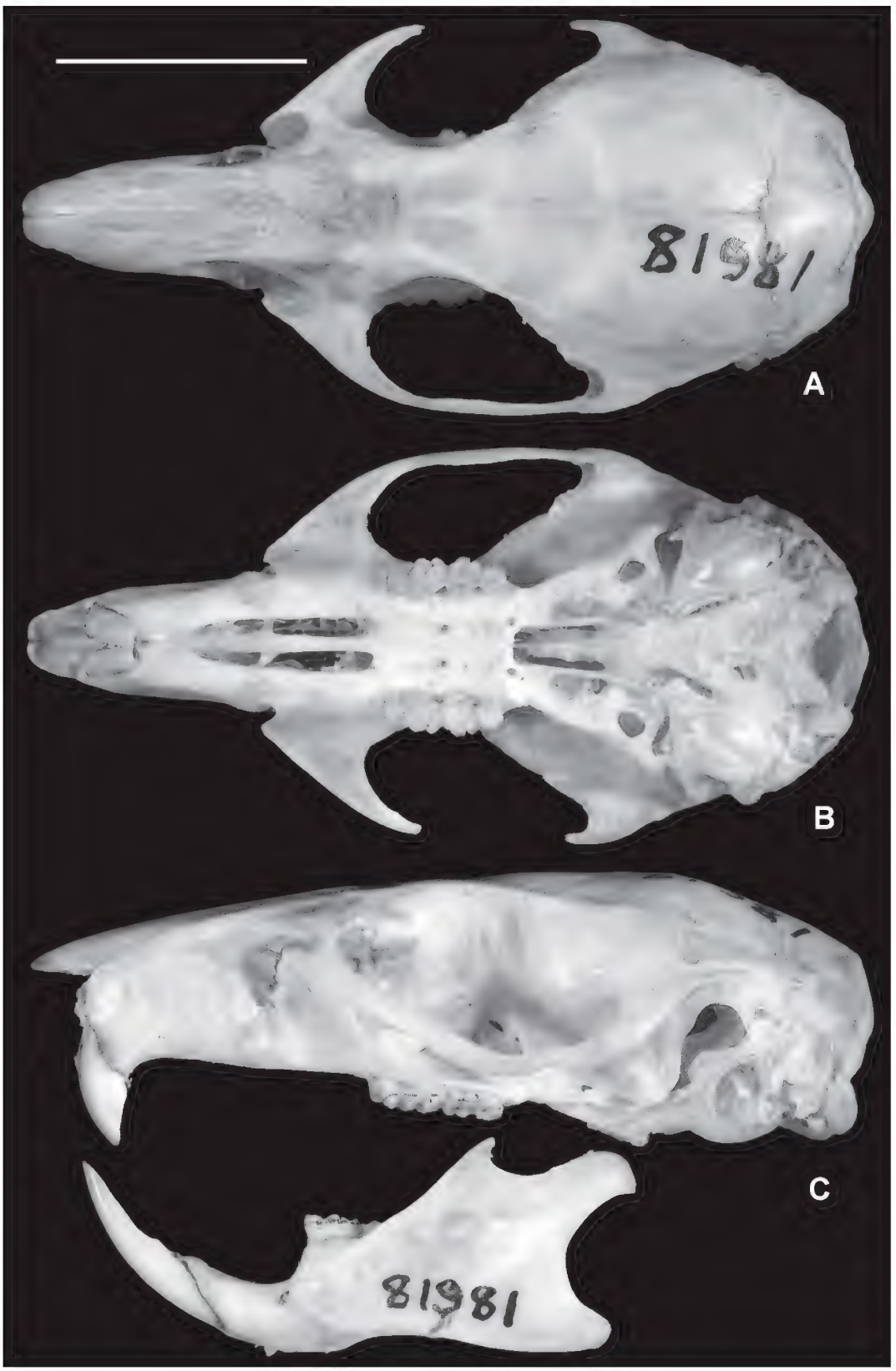

Fig. 2. *Praomys coetzeei* n. sp., holotype, skull, dorsal view (A), ventral view (B), lateral view (C) (photo R. Banasiak). – Scale: 10 mm.

bergi or *P. misonnei*. The dorsal hairs in the mid back are 9–10 mm. In adult specimens the ventral colour is greyish. Only the top of the hairs is white and the basis has a grey colouration. In some specimens the belly is a bit more white than grey; however it is never as white as in *P. tullbergi*. None of the studied specimens has a complete white patch or stripe on the crest or belly, a character found in most other *Praomys* (including *P. rostratus* and *P. petteri*). The tail is normally unicoloured. Dorsal side of hands and feet covered with white hairs.

There are two pairs of inguinal and one pair of pectoral mammae, 2(1–2).

I have no information on the palatal ridges and the plantar pads of the hind foot.

For measurements of the type and the paratypes see Tab. 1. For measurements of other species in the *P. tullbergi* species-complex see Van der Straeten & Verheyen (1981) (*P. tullbergi* and *P. rostratus*), Van der Straeten & Dieterlen (1987) (*P. misonnei*) and Van der Straeten et al. (2003) (*P. petteri*).

Comparisons

Biometrically *P. coetzeei* is closely related to *P. rostratus* and *P. petteri*, both large species of the *P. tullbergi* complex. During the preliminary studies of the biometrical data I compared the skull and external measurements of all species of the *P. tullbergi* species-complex, using a t-test. *P. coetzeei* is highly significant larger (1 % significance level) than *P. misonnei* and *P. tullbergi* for all measurements with the exception of CHOA.

Compared with *P. petteri*, *P. coetzeei* is highly significant larger for INT, breadth of M^1 and LOTE. *P. coetzeei* is highly significant smaller for HEPA, DIA1, DIA2, LNAS, DIN, ROH, and PCPA.

The most distinguishing measurements between *P. coetzeei* and *P. petteri* are the length of diastema and the interorbital breadth.

Canonical analysis

I executed several canonical analyses but present only two of them. The other analyses were pairwise compari-

Tab. 1. Measurements in mm of holotype (FMNH 81981) and adult specimens of *Praomys coetzeei* n. sp. from Angola. Numbers represent sample size, mean, range and standard deviation, respectively. Measurements used in the canonical analysis are indicated with an *; 20 = analysis one with 20 measurements; 18 = analysis two with 18 measurements.

Code	Variable	Holotype	All adult specimens	20	18
HB	head and body length	130.0	18; 117.8 (90.0–140.0) 10.7	–	–
HL	length of tail	163.0	15; 150.2 (123.0–163.0) 10.8	–	–
HL+N	length of hind foot + nail	26.0	16; 26.5 (24.0–28.0) 1.4	–	–
EL	length of ear	21.0	17; 18.6 (14.0–21.0) 2.3	–	–
GRLE	greatest length of skull	33.10	16; 33.20 (31.30–35.20) 1.62	*	*
PRCO	prosthion-condylion (condylobasal length)	30.30	16; 30.72 (29.30–33.30) 1.19	*	*
HEBA	henselion-basion (basilar length)	26.45	16; 26.51 (25.45–28.40) 0.95	*	*
HEPA	henselion-palation (palatilar length)	14.90	17; 15.06 (14.25–16.25) 0.66	*	*
PAF	length of palatal foramina	7.10	18; 7.28 (6.65–8.00) 0.42	*	*
DIA1	length of diastema	9.75	17; 9.76 (8.95–11.10) 0.63	*	*
DIA2	distance between the anterior border of the alveolus of M^1 and the edge of upper incisor	10.50	17; 10.48 (9.55–11.95) 0.70	*	–
INT	interorbital breadth	5.05	17; 5.12 (4.95–5.55) 0.16	*	*
ZYG	zygomatic breadth on the zygomatic process of the squamosal	15.55	16; 15.39 (14.70–16.35) 0.44	*	*
PAL	palate breadth between M^1–M^1	3.30	16; 3.09 (2.80–3.35) 0.18	–	–
UPTE	length of upper cheekteeth	5.10	18; 5.19 (4.90–5.45) 0.17	*	*
UPDE	breadth of upper dental arch (breadth across M^1–M^1)	6.80	17; 6.33 (5.95–6.80) 0.21	*	*
M^1	breadth of first upper molar (crown breadth)	1.55	18; 1.49 (1.40–1.60) 0.05	*	*
ZYPL	breadth of zygomatic plate	4.00	17; 3.83 (3.40–4.30) 0.27	*	*
BNAS	greatest breadth of nasals	3.30	17; 3.57 (3.25–4.10) 0.24	*	*
LNAS	greatest length of nasals	12.75	17; 12.95 (11.65–14.60) 0.78	*	*
LOTE	length of lower cheekteeth	5.00	18; 4.95 (4.75–5.15) 0.12	*	*
CHOA	breadth of choanae (mesopterygoid fossa)	1.50	17; 1.40 (1.20–1.75) 0.15	–	–
BUL	length of auditory bulla	4.35	16; 4.61 (4.35–4.90) 0.14	*	*
BRCA	braincase breadth	12.60	16; 12.58 (12.00–13.05) 0.31	–	–
DIN	depth of incisors	1.65	17; 1.66 (1.35–1.90) 0.13	*	–
ROH	rostrum height at anterior border of M^1	7.50	17; 7.33 (6.75–7.85) 0.34	*	*
ROB	rostrum breadth at anterior border of zygomatic plate	5.40	17; 5.45 (4.80–5.95) 0.29	*	*
PCPA	distance between the extreme points of coronoid process and angular process	9.50	15; 9.64 (9.05–10.45) 0.44	–	–

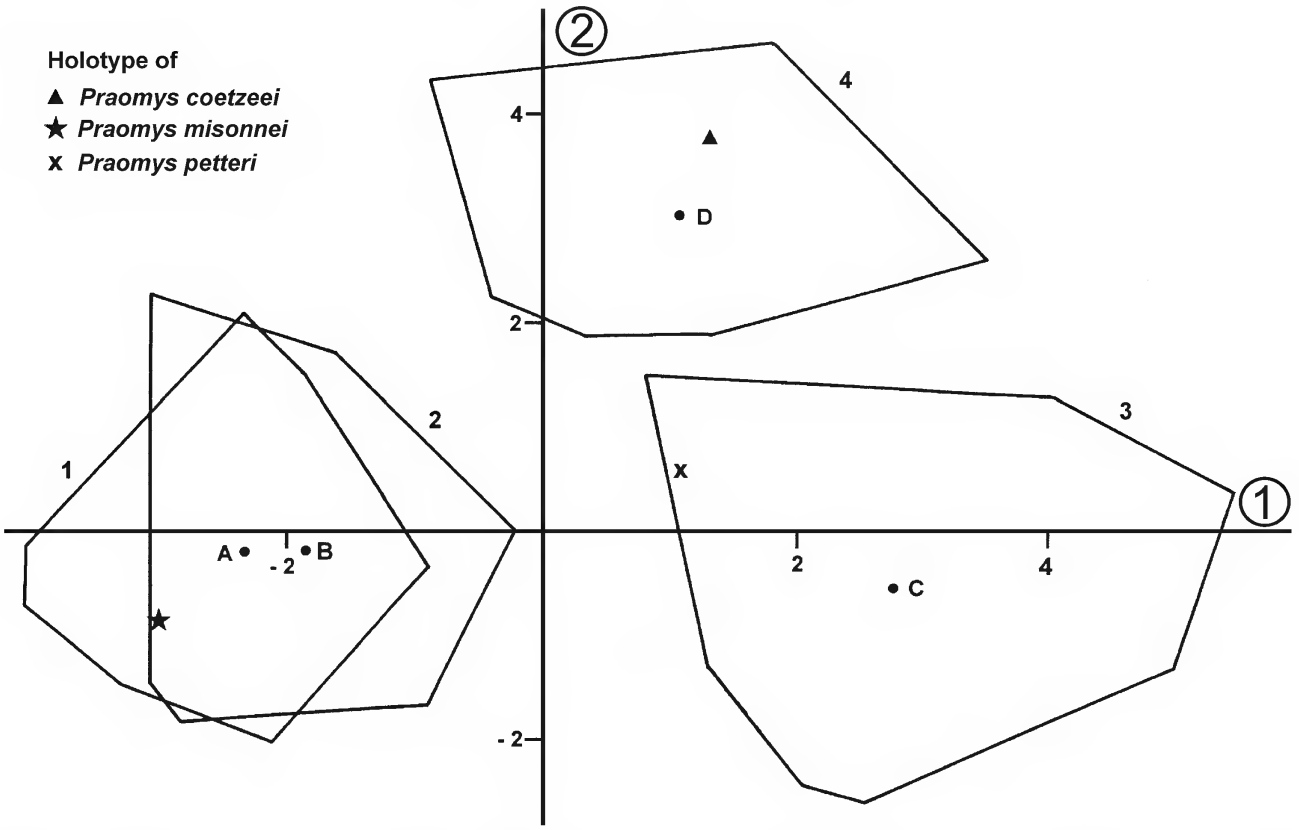

Fig. 3. Canonical analysis of *Praomys* using 20 measurements. Canonical variates 1 and 2; group centroids and extreme limit of each scatter of points are indicated. – 1-A: *P. misonnei* (from Irangi; holotype and paratypes). 2-B: *P. misonnei* (from Batiabongena). 3-C: *P. petteri* (holotype and paratypes). 4-D: *P. coetzeei* n. sp.

sons of the different species, analyses with other combinations of species and with other combinations of measurements. They include discriminant analyses, principle component analyses and correlation analyses. All results were broadly similar.

P. petteri is included in both analyses as this species is biometrically closely related to *P. coetzeei*.

The first analysis focussed on the specimens of *P. coetzeei*, *P. petteri* and *P. misonnei*. In this analyses 20 skull measurements (see Tabs. 1, 2) and 110 specimens were used, divided into four groups: *P. misonnei* from Irangi (holotype and paratypes): 33, *P. misonnei* from Batiabongena: 22, *P. petteri* (holotype and paratypes): 40, and *P. coetzeei*: 15.

In Tab. 2 are given the eigenvectors for the 20 variables, regarding the first two canonical variates. Fig. 3 shows the graphical presentation of the first and second canonical variate, using the eigenvectors of Tab. 2. For each group the centroid and the most extreme values are indicated by a polygonal delimitation. The first canonical variate contains 74.4% of the total variance and the second 19.0%; both together represent 93.4% of the total variation. This analysis shows a clear difference among the three species. There is a good separation between the three different species and an almost complete overlap between the *P. misonnei* specimens from Irangi and Batiabongena. The first canonical variate clearly separates *P. misonnei* from both other species The separation of *P. coetzeei* is mainly caused by the differences following the second canonical variate in combination with the first canonical variate.

The second canonical analysis focusses on the differences between *P. coetzeei*, *P. petteri* and *P. tullbergi*. To optimize the number of *P. tullbergi* specimens only 18 measurements were used (see Tabs. 1, 3). The 86 specimens used, are divided into the following three groups: *Praomys tullbergi* (from Ivory Coast): 30, *Praomys petteri* (holotype and paratypes): 41, and *Praomys coetzeei*: 15.

As the result I give the eigenvectors for the 18 measurements in the two first canonical variates (Tab. 3). The two canonical variate axes contain 78.2% and 21.8% of the variation respectively. The graphical presentation of these two canonical variates is presented in Fig. 4. The first canonical variate clearly separates *P. tullbergi* from the two other species. The second canonical variate separates *P. coetzeei* and *P. petteri* without any overlap.

Tab. 2. Eigenvectors of 20 variables for the first two canonical variates.

Variable symbol	1	2
GRLE	0.0684	-0.0743
PRCO	0.1146	-0.0033
HEBA	0.3028	0.2441
HEPA	0.5487	-0.0930
PAF	-0.1488	0.4271
DIA1	0.4606	-0.2907
DIA2	0.1080	-0.0569
INT	0.0122	0.4404
ZYG	0.1549	0.2025
UPTE	0.0707	0.0704
UPDE	0.0068	0.2733
M^1	0.2467	0.0773
ZYPL	0.3146	0.2457
BNAS	0.0239	0.0224
LNAS	0.3173	0.0194
LOTE	0.1597	0.4467
BUL	0.0737	0.0781
DIN	0.0480	-0.1468
ROH	0.1414	-0.2166
ROB	0.0073	0.0099

Tab. 3. Eigenvectors of 18 variables for the first two canonical variates.

Variable symbol	1	2
GRLE	0.0804	-0.0968
PRCO	0.1084	-0.0589
HEBA	0.4446	0.0853
HEPA	0.4291	-0.2439
PAF	-0.2299	0.3317
DIA1	0.2842	-0.4118
INT	0.1401	0.4862
ZYG	0.3262	0.0928
UPTE	0.0640	0.0324
UPDE	0.2134	0.3320
M^1	0.2305	-0.1784
ZYPL	0.0799	0.1457
BNAS	-0.1864	0.0300
LNAS	0.2162	-0.1229
LOTE	0.2781	0.3590
BUL	0.1456	-0.0125
ROH	-0.2254	-0.2924
ROB	-0.0203	-0.0314

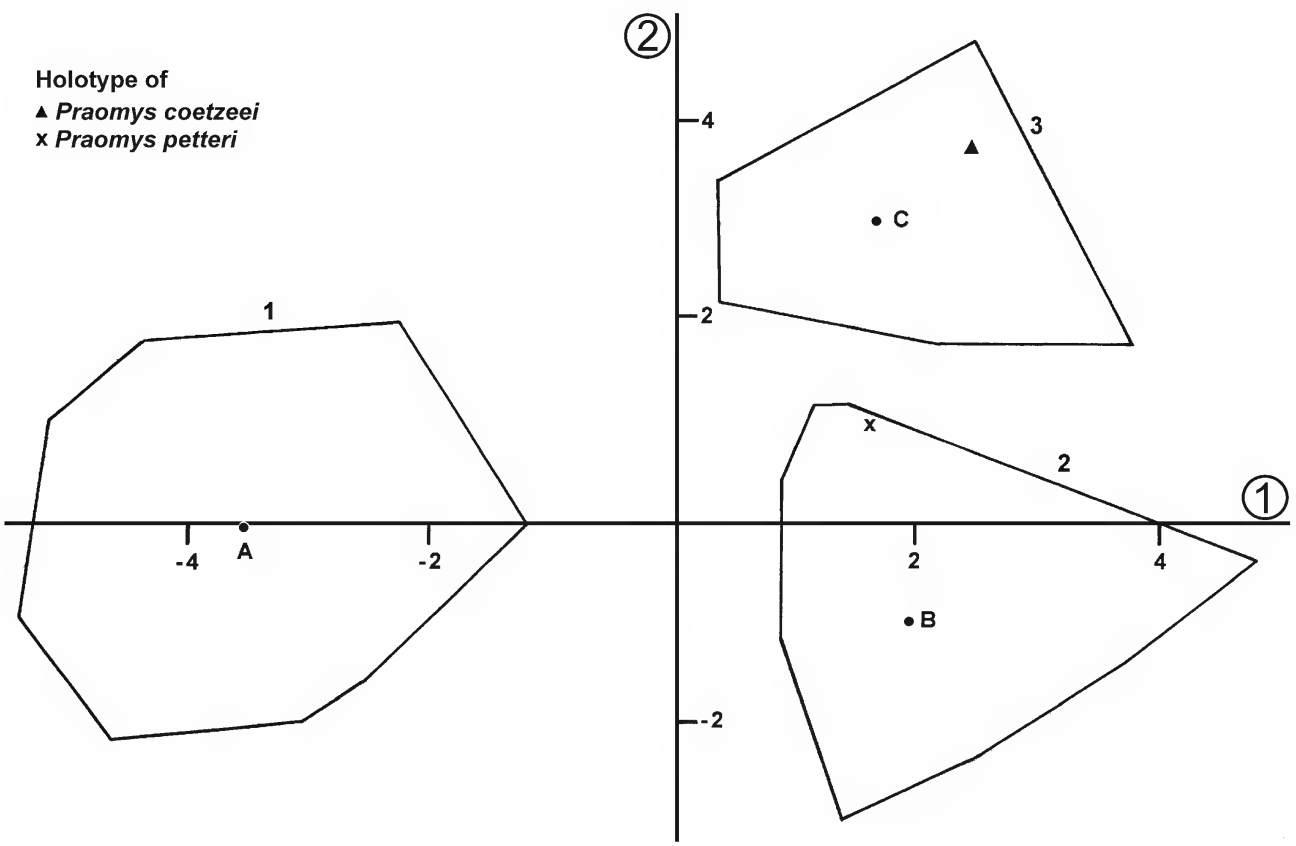

Fig. 4. Canonical analysis of *Praomys* using 20 measurements. Canonical variates 1 and 2; group centroids and extreme limit of each scatter of points are indicated. – 1-A: *P. tullbergi* (from Ivory Coast). 2-B: *P. petteri* (holotype and paratypes). 3-C: *P. coetzeei* n. sp.

In both analyses *P. coetzeei* is clearly separated from the others. From these analyses it is clear that on biometrical characteristics *P. coetzeei* cannot be identified as one of the described species of the *P. tullbergi* species-complex.

4 Discussion

The description of *Praomys coetzeei* brings the number of species within the *P. tullbergi* complex to eight: *P. coetzeei*, *P. hartwigi*, *P. misonnei*, *P. morio*, *P. obscurus*, *P. petteri*, *P. rostratus* and *P. tullbergi*. *P. hartwigi* and *P. obscurus* have a very restricted distribution as they are only known from Mount Oku in Cameroun and Gotel Mountains in Nigeria. The other species can be separated in a larger and a smaller form. The smaller species are *P. misonnei*, *P. morio* and *P. tullbergi* which have an allopatric distribution. *P. coetzeei*, *P. petteri* and *P. rostratus* belong to the large form. These are sibling species with an allopatric distribution. *P. rostratus* is present in all forest zones west of the Dahomey gap (from Ghana to Senegal). The skulls of the *P. rostratus* specimens become larger going from east to west. The exact distribution of *P. petteri* is unknown. Specimens were found in Cameroun, Congo and the Central African Republic. For the moment no specimens are known from Nigeria and the Democratic Republic of Congo. *P. tullbergi* was captured together with *P. rostratus* (for example in Adiopodoumé, Ivory Coast) and with *P. petteri* and *P. jacksoni* (Van der Straeten et al. 2003). *P. coetzeei* is the only species of the *P. tullbergi* complex found south of the Congo river and is for the moment only known from the northwest of Angola. In the collections of the kmMA there are no specimens of the *P. tullbergi* complex collected south of the Congo river. An important *Praomys* collection from Kikwit (Democratic Republic of the Congo; 245 specimens) only contains *P. jacksoni* (Van der Straeten in Leirs et al. 1999). So it seems that *P. coetzeei* has a very restricted distribution.

Van der Straeten & Dudu (1990) recognized four different species-complexes within the genus *Praomys*: the *P. jacksoni* complex, the *P. tullbergi* complex, the *P. delectorum* complex, and the *P. lukolelae* complex. Each of these species-complexes is clearly defined and well marked. A molecular study of a subset of lowland forest species (Nicolas et al. 2005) also supported the first two complexes. The *P. tullbergi* complex consists of eight species. Also, for the *P. jacksoni* complex the number of species is eight: *P. degraaffi*, *P. jacksoni*, *P. minor*, *P. montis*, *P. mutoni*, *P. peromyscus*, *P. sudanensis* and *P. viator*, with at least one undescribed species (Van der Straeten & Kerbis Peterhans 1999). The *P. delectorum* species-complex contains four species, *P. delectorum*, *P. melanotus*, *P. octomastis* and *P. taitae*, and the *P. lukolelae* species-complex has two species including *P. lukolelae* and *P.*

Tab. 4. Geographical data of the localities.

Country	Locality	Geographical coordinates
Angola	Dundo (included Parque Carrisso)	7°22'S 20°50'E
	Duque de Bragança (25 km N – 15 km E)	± 8°52'S 16°03'E
	Gabela (30 km S)	± 11°01'S 14°27'E
	Luhanda	9°14'S 17°12'E
	Sanza Pombo	7°19'S 16°01'E
	Uige	7°37'S 15°03'E
Cameroun	Metet	2°11'N 11°00'E
	Mieri-Bimba	4°15'N 13°59'E
	Nkolbisson	3°51'N 11°37'E
	Yaoundé	3°52'N 11°31'E
	Yokadouma	3°26'N 15°06'E
	Zoatoupsi	3°49'N 11°23'E
Congo (Brazzaville)	Béna	4°02'S 11°50'E
	Kuilele	not located
	M'Bila	3°12'S 13°20'E
	Ménengué	4°16'S 11°47'E
	Tchissanga	4°32'S 11°46'E
Côte d'Ivoire	Adiopodoumé	5°19'N 4°08'W
	Lac Lallié	5°15'N 4°08'W
	Lamto	6°12'N 4°58'W
République Centrafricaine	Boukoko	3°54'N 17°56'E
	Ngueguey	not located
République Démocratique du Congo	Batiabongena	0°36'N 25°13'E
	Irangi	1°54'S 28°27'E

verschureni. This means that the genus *Praomys* contains 22 species, but not all are recognized by MUSSER & CARLETON (2005).

5 Geographical data of the localities

The geographical data of the localities mentioned in the present paper are listed in Tab. 4. The arrangement is alphabetical.

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Manuscript received: 15.V.2007, accepted: 4.X.2007.

Limax (Limax) brandstetteri n. sp. – ein neuer Hochgebirgsschnegel aus den Abruzzen (Gastropoda: Limacidae)

Limax (Limax) brandstetteri n. sp. – a new high mountain slug from the Abruzzi Mountains (Gastropoda: Limacidae)

Gerhard Falkner

Abstract

A new slug, *Limax (L.) brandstetteri* **n. sp.**, from the Maiella massif in the Abruzzi Mountains (central Apennines, Italy) is described. It belongs to the group of black high mountain slugs. The new species differs from the only previously known species of this group from the Apennines, *Limax ianninii* Giusti, 1973, by the formation of a papilla which is perforated by the vas deferens at its entrance into the lumen of the penis. This structure is interpreted as a rudimentary penial papilla. Further differences are the different form of the penial comb and the missing papillar structure on the inner wall of the penis. The preliminary molecular phylogeny (based on 613 nucleotides of the mitochondrial gene COI) in the frame of the Munich *Limax*-project confirms the specific distinctness.

Keywords: *Limax brandstetteri*, new species, *Limax maximus*-group, Appennino Abruzzese, Maiella, endemic species, penial morphology.

Zusammenfassung

Ein neue Nacktschnecke, *Limax (L.) brandstetteri* **n. sp.**, aus dem Maiella-Massiv in den Abruzzen (Zentral-Apenninen, Italien) wird beschrieben. Sie gehört zum Lebensformtyp der schwarzen Hochgebirgsschnegel. Die neue Art unterscheidet sich von der bisher einzigen aus den Apenninen bekannten Art dieses Typs, *Limax ianninii* Giusti, 1973, durch die Ausbildung einer vom Vas deferens an dessen Einmündung durchbohrten Papille, die als rudimentäre Penispapille gedeutet wird. Weitere Unterschiede bestehen in der Ausbildung des Peniskamms und dem Fehlen der Papillenstruktur auf der Innenwand des Penis. Die vorläufige molekulargenetische Analyse (basierend auf 613 Basenpaaren des mitochondrialen COI-Gens) im Rahmen des Münchner *Limax*-Projekts bestätigt die artliche Selbständigkeit.

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1 Einleitung

Während entomologischer Studien und Aufsammlungen von Gehäuseschnecken durch A. Kapp und C. M. Brandstetter (KdW) in der Maiella (Abruzzen) im Mai 2003 hat letzterer in bedeutender Höhe und in weitgehend kahlem Gelände am Rand eines Schneeflecks einen *Limax* beobachtet und photographiert, der sich durch seine einfarbig schwarze Oberseite als typisches Hochgebirgstier zu erkennen gab. Beide Forscher erinnerten sich, derartige Tiere schon bei früheren entomologischen Fachexkursionen im Gebiet beobachtet zu haben. Die einzige bekannte und benannte Art dieses charakteristischen Lebensformtyps im ganzen Gebirgszug der Apenninen liegt bisher aus den Monti Reatini (Latium) vor und soll nach einer sehr allgemein gehaltenen Notiz bei Manganelli et al. (1995: 44) auch im Gran Sasso vorkommen. Bei der Beschreibung dieses *Limax ianninii* Giusti, 1973 hat der Autor (1973a: 488; zum korrekten Publikationsdatum siehe Manganelli et al. 1998: 153) die Einzigartigkeit des Vorkommens in den Monti Reatini betont: „Una accurata indagine bibliografica non mi ha consentito di trovare citazioni, per nessun'altra località appenninica, di limacidi che, anche se attribuiti ad altra specie, presentassero caratteristiche simili alla nuova specie.“ [= Eine genaue bibliographische Nachforschung hat es mir nicht erlaubt, für irgendeine andere apenninische Lokalität Angaben von Limaciden zu finden, die, auch wenn sie anderen Arten zugeordnet wären, Merkmale aufgewiesen hätten, die der neuen Art ähnelten.]. In der Maiella war also – nach den

Monti Reatini und dem Gran Sasso – ein drittes derartiges Vorkommen festgestellt worden und damit verbreitungsmäßig oder sogar taxonomisch etwas Neues zu erwarten.

Auf meine Bitte hin hat C. M. Brandstetter dann im Mai 2005 eine weitere Expedition in die Maiella unternommen, die speziell der Suche nach diesem schwarzen Hochgebirgsschnegel galt. Nach anfänglich vergeblichen Tagprospektionen konnte er schließlich, mit Unterstützung der lokalen Bevölkerung und Jeeps der Jagdgenossenschaft, die mit starken Scheinwerfern ausgerüstet waren (normalerweise zur Wildschweinjagd), eine Nachtexkursion durchführen, während der im Scheinwerferlicht zahlreiche Tiere gefunden wurden.

Abkürzungen der Institutionen

IZSI	Istituto di Zoologia dell'Università di Siena
KdW	Gesellschaft zur Kartierung der Wirbellosen in Vorarlberg und Liechtenstein, Bürs
SMNS	Staatliches Museum für Naturkunde, Stuttgart
ZSM	Zoologische Staatssammlung, München

Dank

An erster Stelle danke ich Clemens M. Brandstetter, der mir das kostbare Material zur Bearbeitung anvertraut hat. Den institutionellen Rückhalt fand ich als ehrenamtlicher Mitarbeiter im Staatlichen Museum für Naturkunde Stuttgart durch den Kustos Hans-Jörg Niederhöfer, der auch technische Hilfe durch Annette Schultheiss und redaktionelle Betreuung durch Hans-Peter Tschorsnig vermittelte. Die DNA-Analyse eines Tiers der neuen Art verdanke ich Barbara Klee im Rahmen des Münchner *Limax*-Projekts an der Zoologischen Staatssammlung München. Der Projektleiter Gerhard Haszprunar und Barbara Klee gestatteten freundlicherweise die Vorabpublikation eines Ausschnitts aus dem umfangreichen vorläufigen *Limax*-Stammbaum. Alessandro Hallgass hat dem Stuttgarter Museum das Vergleichsmaterial aus dem Gran Sasso zur Verfügung gestellt. Die gewohnte selbstlose Hilfe bei allen Dokumentationsaufgaben und der Manuskripterstellung erhielt ich trotz andauernden Krankenlagers von meiner Frau Margrit. Für die Begutachtung des Manuskriptes danke ich Hans-Jörg Niederhöfer und einem anonymen Gutachter.

2 Material

Das der Beschreibung von *Limax brandstetteri* n. sp. zugrunde liegende Material ist in Kapitel 3 aufgelistet. Von zwei anderen Arten (bzw. Artengruppen) lag das nachfolgende Vergleichsmaterial vor:

Limax ianninii: Italien, Monti Reatini, zwischen Monte Terminillo und Monte Elefante, ca. 2000 m (Fundstelle 09), leg. C. M. Brandstetter, 19.VIII.2006 (KdW); DNA-taugliche Gewebeproben von der rechten Seite des Mantelschilds befinden sich unter den Nummern L811–L813 in der ZSM. – *L.* cf. *ianninii*: Italien, Gran Sasso, Comune di Pietracamela, loc. Campo Pericoli (Prov. Téramo), 2300 m, leg. A. Hallgass, 16.VI.2007 (SMNS ZI 0055739); DNA-Probe SMNS ZI 0067950.

Limax maximus s. lat.: *L.* sp. (*maximus*-Gruppe), Italien, Maiella, Foro-Tal, leg. C. M. Brandstetter, 1.XII.2004 (SMNS ZI 0066225); DNA-Proben L213 und L214 in der ZSM. – *L.* sp. (*maximus*-Gruppe), schwarze Morphe, Italien, Maiella, Umgebung Lettomanoppello (Prov. Pescara), leg. Famiglia di Peppino (Ristorante La Pietra Carrata), 24./25.V.2005 (SMNS ZI 0055737); DNA-Probe L308 in der ZSM. – *L.* sp. (*maximus*-Gruppe), braune Morphe, Italien, Maiella, Umgebung Lettomanoppello (Prov. Pescara), leg. Famiglia di Peppino (Ristorante La Pietra Carrata), 24./25.V.2005 (SMNS ZI 0055736); DNA-Probe L316 in der ZSM. – *L.* sp. (*maximus*-Gruppe), violett-anthrazitfarbene Morphe mit feinen Punkten, Italien, Maiella, Lettomanoppello (Prov. Pescara), leg. C. M. Brandstetter, 28.V.2005 [Tier abgestorben, nicht aufbewahrt]; DNA-Probe L318 in der ZSM. – *L.* sp. (*maximus*-Gruppe), einfarbig graue Morphe, Italien, Maiella, Lettomanoppello (Prov. Pescara), leg. C. M. Brandstetter, 28.V.2005 (SMNS ZI 0055738); DNA-Probe L319 in der ZSM. – *L.* sp. (?*maximus*-Gruppe), Italien, Monte Cimino, leg. G. Falkner und C. M. Brandstetter, 1.VII.2005 (SMNS ZI 0066224); DNA-Probe L346 in der ZSM. – *L. maximus* Linnaeus, 1758, Italien, Chiavenna, Borgonuovo (Prov. Sondrio), leg. C. M. Brandstetter, 29./30.VII.2005 (SMNS ZI 0066210, SMNS ZI 0066229); DNA-Probe L453 in der ZSM. – *L. maximus*, Italien, Siena, Strada di Pescaia, leg. G. Falkner und C. M. Brandstetter, 27.X.2005 (SMNS ZI 0066226); DNA-Probe L455 in der ZSM. – *L. maximus*, Großbritannien, Schottland, östlich Perth, Kinfauns Castle, leg. G. und M. Falkner, 25.VII.2004 (SMNS ZI 0066230). – *L. maximus* 1 Exemplar P-Tier + 3 Exemplare F1-Tiere, schwarzbraune Morphe, Großbritannien, Schottland, Quarrymill Park, leg. G. und M. Falkner, 25.VII.2004 (SMNS ZI 0066231–0066232); DNA-Probe L293 in der ZSM. – *L. maximus*, Schweden, Prov. Skåne, Östra Karup, leg. T. von Proschwitz, 27.X.2005 (SMNS ZI 0066233); DNA-Probe L448 in der ZSM.

3 Beschreibung von *Limax brandstetteri* n. sp.

Material

Holotypus: Italien, Latium, Abruzzen, Maiella, Maielletta, Gemeindegebiet Lettomanoppello (Prov. Pescara), 1750 m, leg. C. M. Brandstetter, 27.V.2005, Nachtexkursion (SNMS ZI 0066214). Eine Gewebeprobe für DNA-Analyse befindet sich unter der Nummer L309 in der ZSM.

Paratypen: 32 Exemplare, gleiche Funddaten wie der Holotypus (SNMS ZI 0066211–0066213, 0066215–0066222). – 2 Exemplare, gleiche Funddaten wie der Holotypus (Coll. Giusti, IZSI). – DNA-Proben L320 und L765–L766 in der ZSM.

F1-Exemplare (SMNS ZI 0055740, 0066533; DNA-Proben L767–768 in der ZSM) werden nicht zur Typusserie gerechnet.

Derivatio nominis

Nach dem Entdecker der Art, Herrn Clemens M. Brandstetter, Bürs, in freundschaftlicher Verbundenheit. Nach einem eher zufälligen initialen Indiz ist die Auffindung dieser Art, die sich im Verlauf weiterer Untersuchungen als neu herausstellte, das Resultat einer mit Zähigkeit durchgeführten, breit angelegten und gezielten Geländeforschung. Diese Leistung soll durch die Namengebung gewürdigt werden.

Diagnose

Eine Art des Genus *Limax* Linnaeus, 1758, *maximus*-Gruppe (*Limax* s. str.), die zum Morphotyp der reliktären schwarzen Hochgebirgsformen Mittelitaliens gehört und sich von der einzigen bisher beschriebenen Art, *Limax ianninii* Giusti, 1973, durch schlankeren Penis, gut ausgebildetes Peniscoecum, eine rudimentäre vom Vas deferens durchbohrte Penispapille, eine andere Struktur der Penisinnenwand und einen im unteren Teil höheren Peniskamm, dem äußerlich eine deutliche Auftreibung entspricht, unterscheidet.

Äußere Merkmale

Eine kleine, bis höchstens mittelgroße *Limax*-Art, oberseits überwiegend tiefschwarz, sehr selten schwärzlichbraun oder -grau, mit einfarbig weißlich-cremefarbener Sohle (Abb. 1–5). Mit zunehmendem Alter stellt sich eine leichte Andunkelung der randlichen Sohlenfelder ein. Der Mantelschild ist relativ kurz mit stumpf gewinkeltem Hinterrand; der kurze farblich nicht abgesetzte Kiel reicht etwa über ein Viertel der Rückenlänge; im vorderen Drittel des Rückens lassen sich 32 bis 38 manchmal undeutlich separierte Runzelreihen zählen. In Ruheposition kontrahiert, sind die Rückenrunzeln auffallend scharf und deutlich geschlängelt.

Auffallend ist, dass sich die Tiere außerordentlich lang und schmal strecken können und die Messung der Länge „gestreckt kriechend" vom Körpervolumen her deshalb kein mit anderen *Limax*-Arten vergleichbares Maß darstellt. Die adulten Tiere messen gestreckt kriechend 9,5–12,5 cm, Rückenbreite 1,0–1,5 cm, Sohlenbreite 1,2–1,7 cm. In der F1 wurden die Tiere bis zur Geschlechtsreife nur 8,5–10,0 cm lang.

Maße des Gehäuserudiments (Schälchen): Länge 9,0–10,0 mm, Breite 6,0 mm; der innere verkalkte Bereich ist bei dem abgebildeten Schälchen (Abb. 13) 8,3 mm lang und 3,8 mm breit.

Genitalapparat

Die Zwitterdrüse ist langoval und liegt bei protandrischen und jugendlich-reifen Tieren im Ende des Eingeweidesacks; bei älteren Tieren und gegen Ende der Legeperiode verkleinert sie sich und wird von der Mitteldarmdrüse umschlossen. Zwittergang und Spermovidukt bieten keine taxonomisch relevanten Besonderheiten; die eiweißproduzierenden Organe, Eiweißdrüse und weiblicher Teil des Spermovidukts (Uterus), verändern sich stark mit Reife und Funktionszustand (vergleiche z. B. Abb. 12 und 14a). Auffallend ist der kurze freie Ovidukt, der ungefähr halb so lang ist wie Bursa und Pedunculus der Bursa copulatrix zusammen. Der Penis ist kurz und stämmig, 17,0–20,0 mm lang, wenig geschlängelt, mit deutlichem, im obersten Teil „kappenartig" abgesetztem Coecum und einer auffallenden Verdickung im unteren Drittel. Die Penisspitze mit dem Coecum ist leicht blaugrau pigmentiert oder zeigt zumindest einen leichten grauen Anflug. Das dicke kurze Vas deferens ist vor der Einmündung in den Penis stärker verdickt und macht hier einen muskulös drüsigen Eindruck (bei frischen Präparaten opak). Das Vas deferens mündet unmittelbar neben dem Ansatz des Penisretraktors und ist mit wenig Bindegewebe angeheftet, es umschlingt den Penis einmal.

Innenstruktur des Penis (Abb. 14): Bei Öffnung des Penis ergibt sich ein über die ganze Länge durchlaufender stark entwickelter Peniskamm, der im Coecum in mehrere kurze Fortsätze übergeht (wabenartig). Im Bereich der Auftreibung im unteren Drittel, das heißt bei evertiertem Penis im oberen Bereich, ist der Kamm am stärksten entwickelt, am höchsten und vielfach gefaltet. Er ist auf der äußeren Seite über seine ganze Länge regelmäßig und kräftig quergerieft, die innere Seite ist nur andeutungsweise leicht gerieft. Die Riefen gehen gegen die Basis des Kamms in eine feine, wenig auffällige Warzenstruktur über. Die Wandung des Penislumens ist weitgehend glatt mit nur stellenweise schwacher Querriefung. An der Einmündung des Vas deferens befindet sich eine deutlich abgesetzte blasige Papille, die vom Vas deferens durchbohrt wird.

Merkmale des Holotypus

Als Holotypus wurde ein Tier ausgewählt, das im Gelände bei der Auffindung photographiert wurde (Abb. 3). Totalpräparat: SMNS ZI 0066214 (Abb. 11), abgetötet am 6. Juni 2005; die im Leben entnommene DNA-taugliche Gewebeprobe von der rechten Seite des Mantelschilds befindet sich in der ZSM. Es handelt sich um ein tiefschwarzes Tier mit cremefarbiger Sohle. Maße des Präparats: Länge 6,4 cm, Sohlenbreite 0,9 cm, Länge des Mantels 2,2 cm. Der kurze Kiel reicht im Präparat 14,5 mm auf den Rücken; 32 Runzelreihen. In der Genitalentwicklung ist der Holotypus als protandrisch einzustufen: Penis, Zwitterdrüse und Zwittergang sind voll entwickelt, die Zwitterdrüse ist auffallend groß. Länge des Penis 17,5 mm, Breite des Penis 1,9–2,2 mm, an der submedianen Auftreibung 2,9 mm, Länge des Coecums 1,3 mm, Spermovidukt (sehr schwächlich) Länge 13 mm, Breite 2,0 mm, Eiweißdrüse Länge 3,2 mm, Zwittergang 0,6 mm breit, Zwitterdrüse (mächtig entwickelt) 15,0 × 6,4 mm.

Verbreitung

Limax brandstetteri n. sp. ist bisher nur aus einem eng begrenzten Gebiet um La Maielletta zwischen 1750 m (locus typicus) und 2100 m (ein Tier wurde von A. Kapp nahe beim Blockhaus in 2100 m Höhe beobachtet) bekannt. Im Jahr 2003, als die erste Photodokumentation gelang, bewegten sich die Freilandbeobachtungen dieses schwarzen *Limax* zwischen 1800 m (C. M. Brandstetter) und 1950 m (A. Kapp). Das Verbreitungsgebiet liegt im Grenzgebiet zwischen den Provinzen Pescara und Chieti. Es kann als sicher angenommen werden, dass es sich um einen Endemismus des Maiella-Massivs handelt.

Biotop

Limax brandstetteri n. sp. lebt auf weitgehend kahlen, steinigen Alpenrasen, die extensiv beweidet werden. Die Aktivitätsperiode erstreckt sich nach den früheren Beobachtungen und Angaben der ortsansässigen Bevölkerung bis Anfang Dezember. Oft liegt der Schnee bis weit in das Frühjahr hinein und die Schnecken sind dann

Abb. 1–3. *Limax brandstetteri* n. sp., photographiert im Biotop. – **1**. Erstes Tier, Ende Mai 2003 zwischen Blockhaus und der Abzweigung zum Eremo Santo Spirito, 1800 m. **2**. Schreckreaktion mit aufgestelltem Mantel nach Blitzlicht, 27.V.2005. **3**. Holotypus bei Auffindung im Biotop, 27.V.2005. – Etwa natürliche Größe, Photos C. M. Brandstetter.

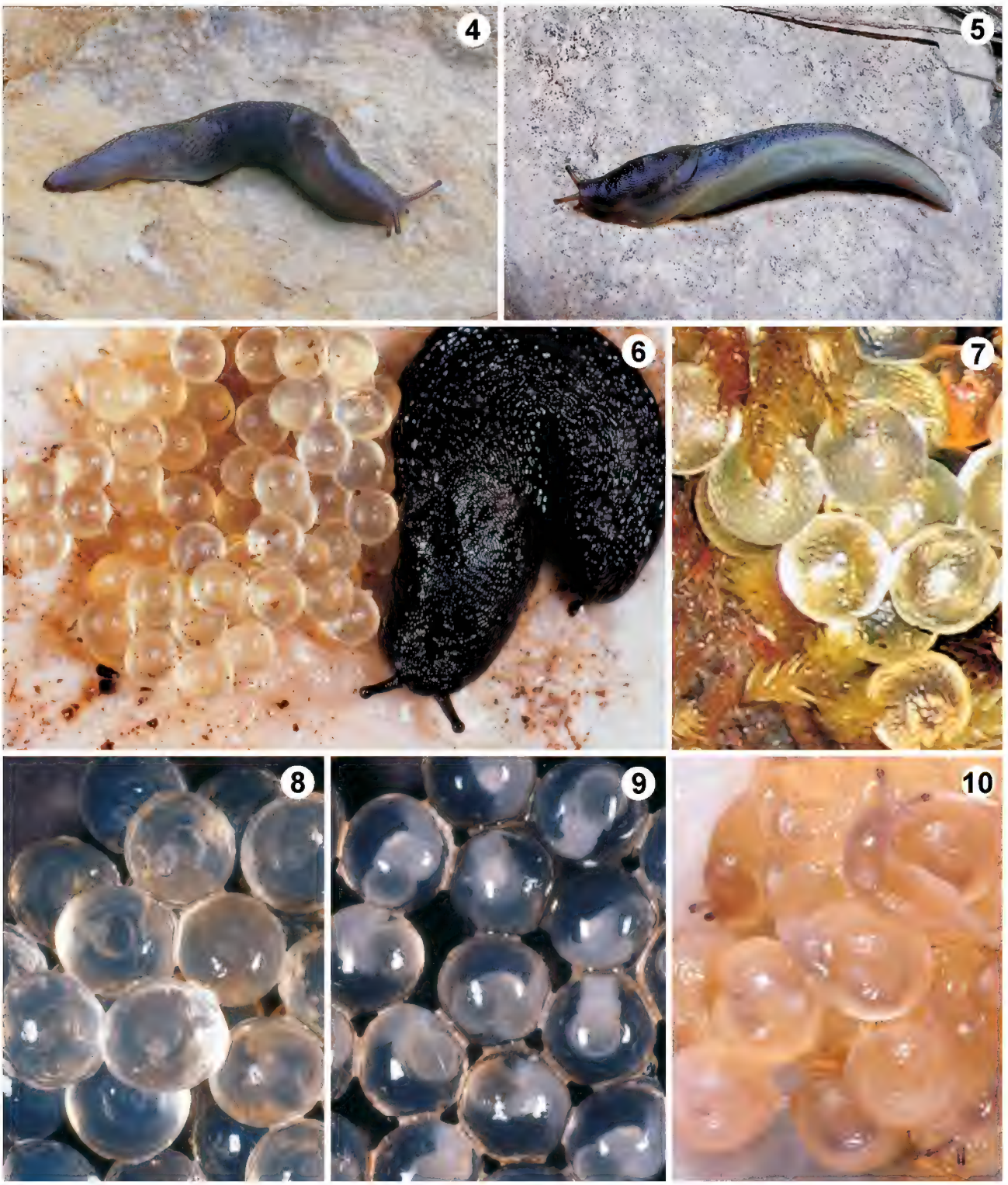

Abb. 4–10. *Limax brandstetteri* n. sp. – **4–5**. Adultes F1-Exemplar, photographiert 11.X.2006 (geschlüpft August 2005, zum Zeitpunkt der Manuskriptabfassung noch am Leben). **6**. Exemplar (gestreckt kriechend Länge 10,5 cm bei 1,1 cm Rückenbreite), das unter der Moosdecke neben einer Ansammlung früher abgesetzter Gelege ruht; der große Eiklumpen umfasst drei Gelege. **7–9**. Gelege in verschiedenen Entwicklungsstadien. **10**. Älteres Gelege, Schlupfbeginn 24.VIII.2005. – Abb. 4–5 etwa natürliche Größe (Photos A. Schultheiss, SMNS), Abb. 6 zweifach, Abb. 7–10 vierfach.

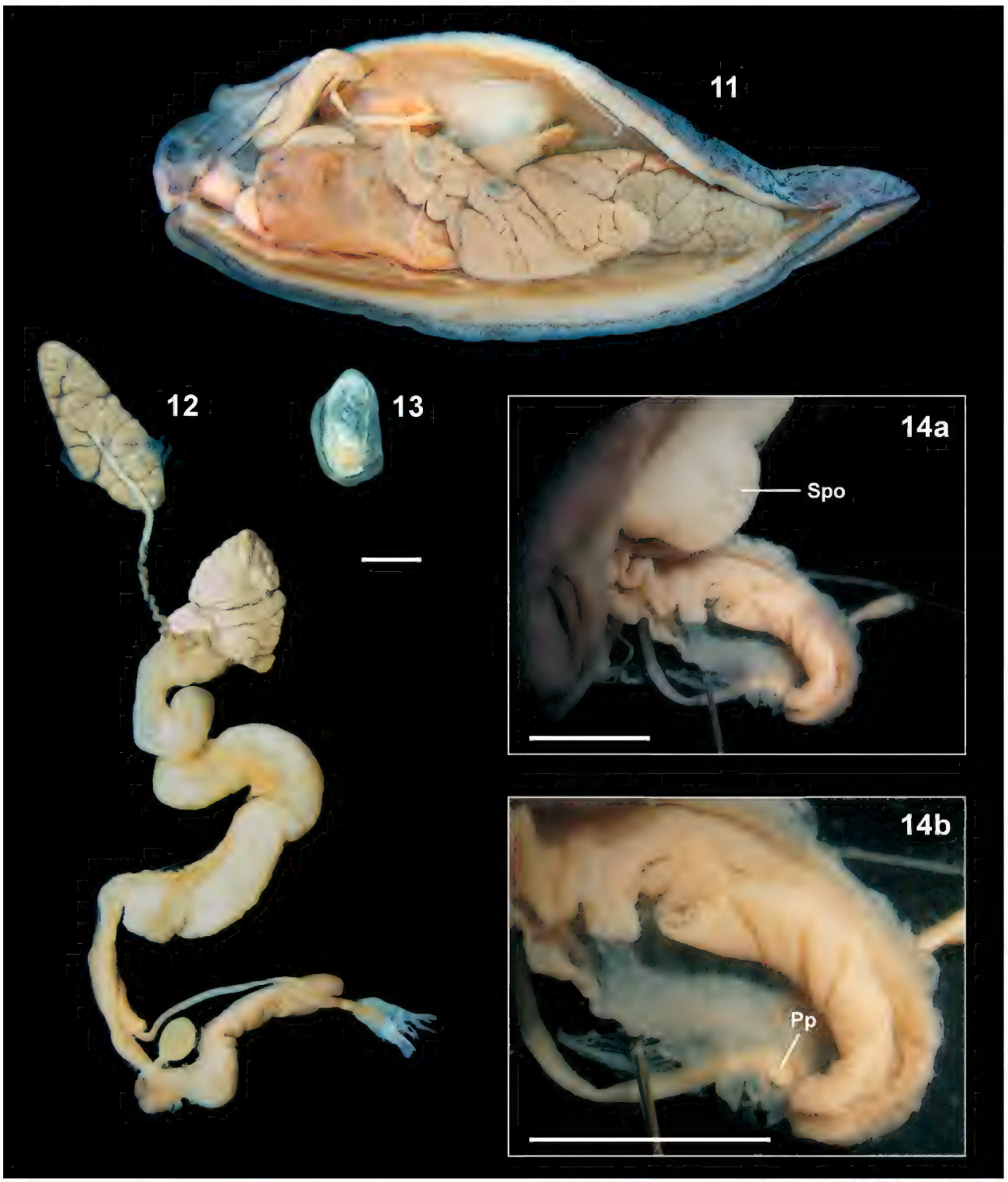

Abb. 11–14. *Limax brandstetteri* n. sp., anatomische Details. – **11**. Holotypus, Präparat geöffnet, Situs der inneren Organe; es handelt sich um ein protandrisches Individuum, weshalb der noch schmächtige weibliche Genitaltrakt verborgen ist. **12**. Genitalapparat eines Individuums im Stadium beginnender Reife der weiblichen Organe. **13**. Schälchen (Gehäuserudiment). **14**. Penis-Innenstruktur, (a) Übersichtsbild (Spo = vollreifer weiblicher Teil des Spermovidukts [Uterus]), (b) Detailbild (Pp = rudimentäre Penispapille). – Maßstrich: 0,5 mm.

bereits auf aperen Flächen in unmittelbarer Nähe des Schneerands aktiv.

4 Phänologie, Lebendhaltung und Fortpflanzung

Altersverteilung und Phänologie

Die im zeitigen Frühjahr unmittelbar nach der Schneeschmelze gesammelte Probe bestand fast zur Hälfte aus adulten reifen Exemplaren, bei denen der Uterus hell durch die Körperwand schimmerte; ein schwaches Viertel der Tiere war subadult (bis protandrisch?); der Rest juvenil, jedoch schon voll ausgefärbt. Es kann also geschlossen werden, dass die Tiere zweijährig sind und sowohl in voll fortpflanzungsfähigem Stadium wie auch als Jungtiere überwintern, wobei durch einen gewissen Anteil akzelerierter oder retardierter Exemplare der genetische Zusammenhang der Generationen aufrecht erhalten wird und gleichzeitig flexible Reaktionen der Gesamtpopulation auf klimatische Extreme möglich werden.

Beobachtungen bei der Haltung

Die Tiere (anfangs 25 Exemplare) wurden in einem großen Terrarium mit einem Rauminhalt von ca. 40 Litern gehalten. Den Boden bildete feuchtes Fließpapier mit Moosdecke. Wildfänge und F1 zeigten sich empfindlich gegen höhere Temperaturen. Nach einem ersten Einbruch bei der Haltung der Wildfänge waren Ende Mai/Anfang Juni durch Hitzeeinwirkung (Raumtemperatur über 30 °C) mehrere Tiere schlagartig abgestorben, viele zeigten Schwäche und alle waren im Bereich des Rückens benagt und zerbissen. Als erste Rettungsmaßnahme wurden mehrere Tiere in Einzelhaltung separiert und im großen Terrarium die Anzahl auf sechs Exemplare reduziert. Die Behälter wurden dann im Keller untergebracht, wo während des Sommers auch bei größter Hitze eine gleichmäßige Temperatur von 15 °C herrscht. Dabei erholten sich die geschädigten Tiere rasch. Nach dem Sommer wurden einige separierte Tiere in der Wohnung gehalten, wo sie sich gut weiterentwickelten, während die im Keller verbliebenen bei sinkender Temperatur retardierten.

Gelege und Entwicklung der Jugendstadien

Von drei adulten Wildfängen wurden insgesamt sieben Gelege (Abb. 6–10) abgesetzt. Der Durchmesser der kugeligen Eier bewegt sich zwischen 4,8 und 5,2 mm, fast alle weisen nur einen Kern auf. Die Oberfläche ist runzlig hammerschlägig (Abb. 7) und nicht spiralgerieft wie bei anderen *Limax*-Arten. Die Eier sind offenbar sehr dünnwandig, so dass kein messbares Innenlumen differenziert werden kann. Die drei frühesten Gelege wurden wahrscheinlich zwischen dem 1. und 4. August 2005 abgelegt, interessanterweise fast an derselben Stelle im Terrarium, so dass ein großer Klumpen aufgefunden wurde. Dieser Bereich muss also nacheinander von drei verschiedenen Tieren als idealer Legeplatz gewählt worden sein. Für die Einzelgelege ließen sich 26, 28 und 41 kugelige Eier ermitteln, die teilweise durch Huminfärbung bernsteinfarben bis bräunlichgelb waren. Im Zeitraum 7.–9. August wurden drei weitere Gelege oberflächennah zwischen dem Moos abgesetzt, wieder zusammen an ein und derselben Stelle, was den Gedanken an intentionelle Legeplatzwahl aufkommen lässt. Diese Gelege bestanden aus 32, 41 und 31 Eiern, ebenfalls kugelig, aber bei Auffindung noch weiß durchsichtig. Am 19. August wurde noch ein siebtes Gelege mit 42 Eiern abgesetzt. Die Stellen mit der Häufung von Gelegen wurden auch bevorzugt als Ruheplätze aufgesucht (Abb. 6).

Bei den drei älteren Gelegen war die Embryonalentwicklung bei der Auffindung (10. August) schon fortgeschritten. Die außerordentlich durchsichtigen kommaförmigen Embryonen hatten eine Länge von 1,0–1,3 mm, der Durchmesser der Kopfblase betrug je nach Entwicklungsstand 1,8–2,6 mm, derjenige der Dotterkugel lag zwischen 0,95 mm und 1,3 mm, war also auffallend klein (Abb. 8). Bei den älteren Embryonen fiel auf, dass die Kopfblase den Mantelschild rechtwinklig nach hinten drückt. Am 21. August waren die Fühler im Ei bereits violett gefärbt (tintig), am 24. August um 15:30 Uhr begann der Schlupf (Hinterende voran, nicht Kopf voran), der am 26. August abgeschlossen war. Die Entwicklung dauert also – unter Laborbedingungen – rund 24 Tage.

Jugendfärbung: Die im Ei beobachtete „tintige“ Farbe der Fühler geht vor dem Schlupf in hellgrau über. Die frisch geschlüpften Tiere zeigen keine Spur von Stammbinden, sind zart dunkel pigmentiert mit etwas dunklerem Mantel und 7,0–8,5 mm lang. Sehr auffallend ist der scharf abgesetzte, lamellenartig vorstehende Kiel.

Eier, Embryonen und Jugendstadien weisen eine Reihe bisher bei *Limax* noch nie beobachteter Besonderheiten auf: (1) hammerschlägige Oberflächenstruktur und dünne, nicht wahrnehmbare Eihülle, (2) anfangs durchsichtiger „glasiger“ Embryo mit extrem großer Kopfblase und kleiner Dotterkugel, (3) in späteren Stadien auffallend rechtwinklig zurückgebogener Mantel, und (4) frisch geschlüpfte Jungtiere mit extrem scharfem lamellenartigen Kiel.

5 Diskussion

Es handelt sich bei *L. brandstetteri* n. sp. bereits nach anatomischem Befund eindeutig um eine neue Art, die sich durch mehrere qualitative Merkmale und Merkmalszustände von der einzigen bisher benannten Art des gleichen Lebensformtyps im gesamten Apenninenzug differenzieren lässt. Auch die molekulargenetische Analyse eines mitochondrialen Genabschnitts (COI, 613 Basenpaare) im Münchner *Limax*-Projekt (Klee 2006: 106)

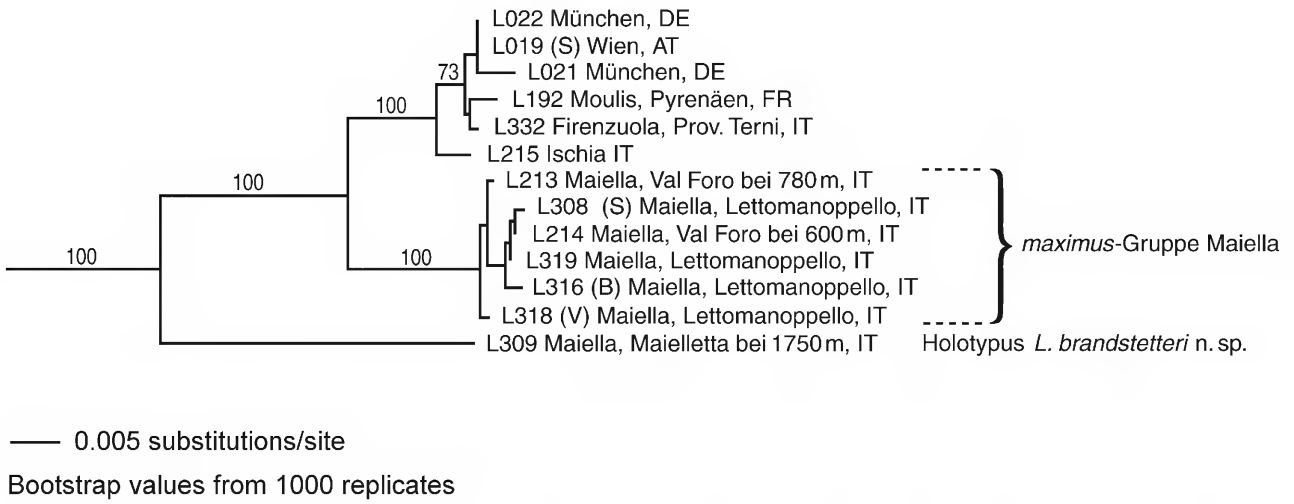

Abb. 15. Die phylogenetische Position der Maiella-Limaces. Stammbaumausschnitt COI-613 bp NJ aus dem Münchner *Limax*-Projekt (unpubliziert, mit freundlicher Erlaubnis von G. Haszprunar und B. Klee). – DE = Deutschland, AT = Österreich, FR = Frankreich, IT = Italien; (S) = schwarze Morphe, (V) = violett-anthrazitfarbene Morphe, (B) = braune Morphe; L … = Probennummern.

erweist die Eigenständigkeit der Art, die im vorläufigen Stammbaum (Abb. 15) sogar als basaler Ast den übrigen Vertretern der *maximus*-Gruppe (*Limax* s. str.) gegenübersteht. Der Stammbaumausschnitt belegt außerdem eine bemerkenswerte Sonderstellung der anderen von C. M. Brandstetter gesammelten Limaces aus der *maximus*-Gruppe. Die Trennung dieser Maiella-Tiere, die unter sich einen ausgeprägten disjunkten Polymorphismus zeigen, von den übrigen Formen ist tief und zeigt, dass hier unbedingt auf Artniveau differenziert werden muss. Bevor jedoch neue, vor allem auch kopulationsbiologische Fakten vorliegen, ist es für diese Gruppe schwierig, zu soliden Neubeschreibungen zu gelangen. Die Einbeziehung zusätzlicher italienischer Populationen wird schließlich zeigen, ob mit der *maximus*-Gruppe der Maiella ein weiteres endemisches Element vorliegt. Es liegt einstweilen nahe, die drei Clades, die sich in diesem Baum-Fragment andeuten als sich überlagernde evolutionäre und zeitliche Straten zu deuten. Das Maiella-Massiv würde sich damit als ein Brennpunkt für die phylogenetische *Limax*-Forschung und besonders für die Aufhellung der Geschichte der *Limax maximus*-Gruppe erweisen.

Möglicherweise steht die neue Art dem äußerlich nicht unterscheidbaren *Limax ianninii* aus den Monti Reatini nahe. Während der gesamte Bauplan des Genitalapparats sehr ähnlich ist und durchaus eine nähere Verwandtschaft begründen könnte, gibt es im Bau des Penis tiefgreifende Unterschiede, die zwar zunächst mit großer Sicherheit die Artselbständigkeit begründen, jedoch sowohl junge Abwandlungen auf Art-Niveau wie auch Charakteristika älterer stammesgeschichtlicher Linien darstellen können. Auffallende Unterschiede zu *L. ianninii* finden sich in der äußeren Gestalt des Penis, der keine obere Auftreibung und ein größeres Coecum zeigt. Im Inneren stellt die starke Entwicklung des Peniskamms im unteren Drittel eine weitere Besonderheit dar, die *L. brandstetteri* n. sp. von *L. ianninii* trennt, bei dem der Peniskamm gerade im oberen Drittel am stärksten ausgebildet ist (was in der mächtigen Auftreibung zum Ausdruck kommt). Eine mit der Ausbildung des Peniskamms korrespondierende Auftreibung liegt bei *L. brandstetteri* n. sp. im unteren Drittel. Die Oberflächenstruktur von Peniskamm und Peniswand ist grundverschieden, die für *L. ianninii* beschriebene Papillenstruktur fehlt beispielsweise bei *L. brandstetteri* n. sp. vollständig.

Die von Giusti sowohl bei *L. ianninii* (1973a: 487) als auch bei *L. maximus* aus den Monti Reatini (1973a: 483, Abb. 12) beschriebene „piccola papilla“ an der Einmündung des Vas deferens, sitzt bei *L. ianninii* neben dieser Einmündung, sogar durch einen kleinen Abstand von 0,3–0,4 mm getrennt. Der Porus selbst liegt frei in einer fast glatten, nur fein papillösen Fläche und ist von keinerlei tuberkulösen Erhebungen oder Wülsten umgeben. Die Papille ist blattförmig und wohl eher als Tastorgan oder Reizkörper mit noch unbekannter Funktion zu deuten. Sie dürfte nicht homolog sein mit der erstmals für das Genus *Limax* bei *L. brandstetteri* n. sp. festgestellten Papille, die vom Vas deferens durchbohrt wird und damit eine Struktur darstellt, die bisher noch nie bei *Limax* beobachtet wurde. Es liegt daher nahe, sie als echte rudimentäre Penispapille zu deuten, die einen Hinweis auf eine Stammform mit vollständigem Penis darstellt. Zusammen mit der molekulargenetisch erwiesenen, ausgeprägt basalen und isolierten Stellung im Stammbaum der *L. maximus*-

Gruppe (siehe Abb. 15) ist es verlockend, in *L. brandstetteri* n. sp. eine reliktäre Urform zu sehen, die sich unter ökologischen Extrembedingungen im Hochgebirge erhalten hat. Die noch ausstehende molekulargenetische Untersuchung von *L. ianninii* kann dieses Szenario bestätigen oder widerlegen.

Die Beschreibung und Abbildung der „piccola papilla" bei *Limax maximus* aus den Monti Reatini sind leider unklar und lassen keinen Vergleich mit der durch eigene Untersuchung festgestellten Situation bei den beiden schwarzen Hochgebirgsformen zu. Davon abgesehen ist ein Vorkommen von *L. maximus* in Naturbiotopen größerer Höhen (das von Giusti studierte Material stammte aus Meereshöhen von 1300–1700 m) ziemlich unwahrscheinlich. Die taxonomische Position der Tiere aus den Monti Reatini sollte daher überprüft werden.

Ein ad hoc durchgeführter Vergleich der Einmündungssituation des Vas deferens in der *L. maximus*-Gruppe ergab keine mit *L. brandstetteri* n. sp. vergleichbaren Bildungen. Bei Tieren aus Nordeuropa (Schottland, Südschweden), Chiavenna und Siena (siehe Materialliste in Kapitel 2) gab es keine als „Papille" zu bezeichnenden Strukturen, vielmehr war die Einmündung des Vas deferens von einem wenig erhabenen, wulstigen Ring sehr unregelmäßiger Tuberkeln umgeben, von denen einer gelegentlich etwas vergrößert war. Bei einem Tier vom Monte Cimino waren keine ringförmig angeordneten Tuberkeln vorhanden und auch keine Spur einer irgendwie gearteten Papille. Das Vas deferens mündete vielmehr als ein einfacher Porus in einer glatten Fläche. Ebenso bemerkenswert ist die Situation bei Tieren aus dem Foro-Tal in der Maiella: Das Vas deferens mündet hier an der terminalen Ansatzstelle des Peniskamms und wird vom Peniskamm trichterförmig umfasst, man könnte es auch so beschreiben, dass der Peniskamm mit einer Drehung in das Vas deferens hinein verläuft, wo er sich dann verliert. Den akzessorischen Bildungen an der Einmündung des Vas deferens, die funktionsmorphologisch von größter Bedeutung für den erfolgreichen Austausch des Spermas sind, sollte bei zukünftigen Untersuchungen erhöhte Aufmerksamkeit zuteil werden.

6 Bemerkungen zur subgenerischen Stellung von *Limax brandstetteri* n. sp.

Die hier vorgenommene Zuordnung der neuen Art zum Subgenus *Limax* s. str. kann auf zweierlei Weise gedeutet werden und bedarf einer Erläuterung. Wiktor hat in verschiedenen neueren Arbeiten (z. B. 1989: 172; 1996: 82, hier mit ausführlicher Begründung; 2001: 82) für eine systematische Stellung von *Limacus* Lehmann, 1864, als Subgenus von *Limax* plädiert, eine Auffassung, der auch Schileyko (2003: 1498) gefolgt ist. Daher umfasst das Genus *Limax* bei diesen Autoren zwei Subgenera. Neben dieser Systematik, die weithin immer noch als Standard akzeptiert wird, behandeln italienische Autoren (Giusti 1973b: 201; Manganelli et al. 1995: 21) und die CLECOM-Gruppe [CLECOM = Check-List of the European Continental Mollusca] (Falkner et al. 2001: 52; Bank et al. 2001: 96; siehe bereits Falkner 1991: 103) *Limacus* als selbständiges Genus und gliedern *Limax* dementsprechend nicht weiter auf. Die Eigenständigkeit von *Limacus* ist inzwischen molekulargenetisch erwiesen (Klee et al. 2005: 78 [75]). Warum also noch (oder wieder) Subgenus *Limax* s. str.? Die zuletzt zitierte Veröffentlichung deutet bereits an, dass sich im monophyletischen Genus *Limax* gegeneinander abgegrenzte Gruppen feststellen lassen, die unabhängige evolutive Einheiten darstellen. Diese Erkenntnis ist inzwischen weiter erhärtet worden (Klee 2006) und lässt es sinnvoll erscheinen, das Genus *Limax* zu untergliedern und statt von verschiedenen „Gruppen" (*maximus*-Gruppe, *cinereoniger*-Gruppe, *strobeli*-Gruppe, *corsicus*-Gruppe u. s. w.) zu sprechen, benannte Subgenera zu unterscheiden (Klee & Falkner, basierend auf unveröffentlichten Daten). Eine nomenklatorische Revision der einschlägigen Namen der Gattungsgruppe durch Falkner & von Proschwitz ist im Druck. Die Zuordnung zum nominotypischen Subgenus *Limax* s. str. erlaubt es beispielsweise, die systematische Position von *L. brandstetteri* n. sp., der eine phylogenetisch tief getrennte basale Schwestergruppe zu den übrigen Vertretern dieses Subgenus repräsentiert, klar zu kennzeichnen.

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Manuskript eingegangen: 11.X.2007, angenommen: 29.X.2007.

The terrestrial isopod genus *Schizidium* (Isopoda: Oniscidea): Systematics, distribution, morphology

HELMUT SCHMALFUSS

Abstract

A list of all 24 species of *Schizidium* known up to now is given, with synonyms and distribution areas. The Greek species described under *Paraschizidium* (*aegaeum*, *album*, *atticum*, *falkonerae*, *graecum*) are included in *Schizidium*. The morphological conglobation strategies of *Schizidium* are discussed and contrasted to those of *Armadillidium* and *Armadillo*. The different strategies seem to be correlated to certain biotope categories and their predator spectra.

Keywords: Isopoda, Oniscidea, *Schizidium*, systematics, distribution, functional morphology.

Zusammenfassung

Die bis heute bekannten 24 *Schizidium*-Arten werden aufgelistet, für jede Art werden Synonyme und Verbreitungsgebiete angegeben. Die griechischen Arten, die unter dem Gattungsnamen *Paraschizidium* beschrieben worden sind (*aegaeum*, *album*, *atticum*, *falkonerae*, *graecum*), werden als *Schizidium*-Arten betrachtet. Die morphologischen Einrollstrategien von *Schizidium* werden analysiert und mit denen von *Armadillidium* und *Armadillo* verglichen. Die verschiedenen Strategien scheinen mit bestimmten Biotop-Kategorien und deren Prädatoren-Spektren korreliert zu sein.

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1 Introduction

In a number of families of terrestrial isopods (suborder Oniscidea) the strategy of rolling-up the body to a more or less spherical structure has been developed. This has obviously happened several times independently, judging from the systematic relationships of the families concerned (Tylidae: all genera, Synocheta: genus *Buddelundiella* Silvestri, 1897, Cinocheta: many genera). The function of this conglobation is certainly to reduce the predation rate, because in the rolled-up animal the vulnerable ventral parts are sheltered inside the ball and the outside is formed by the heavily sclerotized tergal sclerites. In species living in dry habitats there may be also the effect of reducing dehydration in the rolled-up animal, but this is certainly secondary, as "rollers" exist also in very wet biotopes and even in aquatic isopod groups (family Sphaeromatidae). The presently treated genus *Schizidium* Verhoeff, 1901 belongs to the family Armadillidiidae. All genera and species ascribed to this family are "rollers".

2 Definition of the genus *Schizidium*

The most recent definition of the genus *Schizidium* Verhoeff, 1901 was given in my publication on the Greek species (SCHMALFUSS 2005):

- Cross-section of pereionites semi-circular, indicating complete conglobation abilities.
- Cleft hind-corners of pereion-epimera 1 (schisma).
- Head always with frontal line, with or without lateral parts of interocular line.
- Frontal line continuous or interrupted in the middle.

This diagnosis holds true, however, for all other genera of the family Armadillidiidae possessing a schisma:

- *Eluma* Budde-Lund, 1885, distributed in southwestern Europe, with two species (VANDEL 1962: 756, CRUZ 1991).
- *Ballodillium* Vandel, 1961, known from Balearic island Menorca, one species (VANDEL 1961).
- *Alloschizidium* Verhoeff, 1919, from Italy, Sardinia and Corsica, ten species (TAITI & FERRARA 1996).

– The Greek species of *Paraschizidium* Verhoff, 1918, which all have a schisma, while the type species *P. coeculum* (Silvestri, 1897) does not possess a schisma. Thus, either a new genus has to be erected for the Greek species, or they have to be considered to belong to *Schizidium*.

Even the tuberculated genera *Echinarmadillidium* Verhoeff, 1901, *Cyphodillidium* Verhoeff, 1939, and *Paxodillidium* Schmalfuss, 1985 may belong to this clade, having secondarily changed some of the diagnostic characters.

If the "schismatic" genera are a monophyletic group and not an example of parallel evolution, we can consider them a group that has evolved and spread along the northern shores of the Tethys Sea, with a present-day distribution from the Iberian peninsula to northern Iran. From a morphological point of view there are no possibilities to plead for sister-group relations among the genera listed above; differences in the characters as one ommatidium versus several ommatidia or a two-jointed antennula versus a three-jointed one are autapomorphies of single species or species groups inside the clade. The investigation of molecular data might help to clarify the interrelationships of the genera mentioned. For the time being I will keep those groups that are geographically separated as separate genera (*Eluma*, *Ballodillium*, *Alloschizidium*), but I ascribe the *Paraschizidium*-species described from Greece to the genus *Schizidium*. This fits from a geographical point of view, and the differences are really only size differences and allometric relations which probably have to do with body size.

3 Species presently ascribed to *Schizidium*

In the following list the species are arranged according to their distribution from west to east.

Schizidium sp., undescribed: Greece, northwestern Peloponnese, Panakhaikó Mountain, 1200 m (S. Sfenthourakis, personal communication).

Schizidium hybridum (Budde-Lund, 1896) (syn. *Armadillidium h.*): Greece, Crete and Gávdos S of Crete, and all Aegean islands SE of a line Sámos–Santoríni; Turkey, southwestern Asia Minor (Schmalfuss 2005).

Schizidium sp., affine *tinum*, ♀♀: Greece, southwestern Aegean, islet Velopúla NE of Monemvasía on the Peloponnese (Sfenthourakis 1995).

Schizidium delmastroi Schmalfuss, Paragamian & Sfenthourakis, 2004: Western Crete (Schmalfuss et al. 2004).

Schizidum falkonerae (Sfenthourakis, 1995) (syn. *Paraschizidium f.*): Greece, southwestern Aegean, islet Falkonéra W of island Mílos (Sfenthourakis 1995).

Schizidium atticum (Sfenthourakis, 1992) (syn. *Paraschizidium a.*): Greece, Attica, N of Keratéa (Sfenthourakis 1992).

Schizidium graecum (Schmalfuss, 1981) (syn. *Paraschizidium g.*): Greece, northwestern Aegean, Northern Sporades, island Lekhúsa (Schmalfuss 1981).

Schizidium album (Sfenthourakis, 1995) (syn. *Paraschizidium*

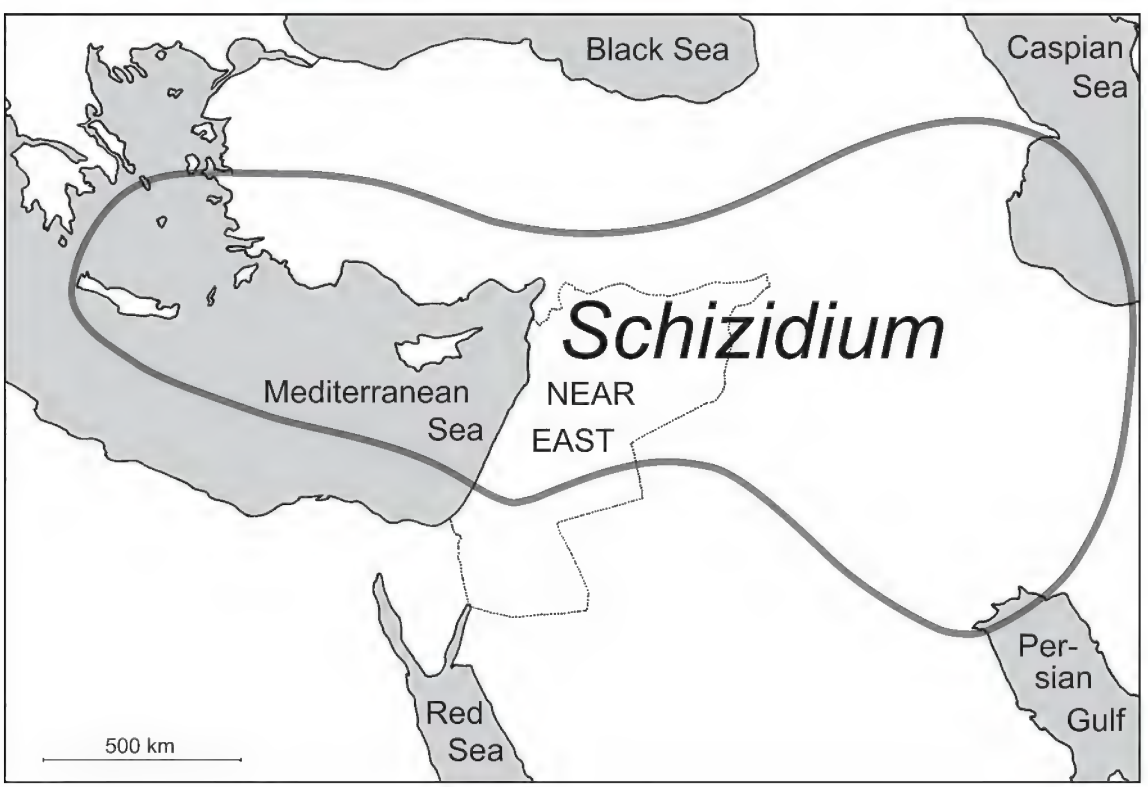


Fig. 1. Distribution area of the genus *Schizidium*.

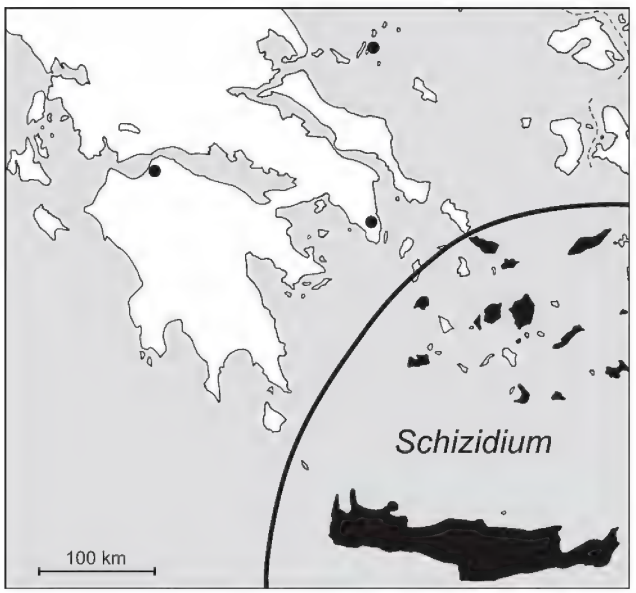


Fig. 2. The present-day distributional boundary of *Schizidium* in the Aegean region, with three relict populations on the Greek mainland and the Northern Sporades.

a.): Greece, central Aegean islands Anánes SW of Mílos, Náxos, Amorgós and Ikaría (SFENTHOURAKIS 1995).

Schizidium aegaeum (Sfenthourakis, 1995) (syn. *Paraschizidium a.*): Greece, Cyclades Islands Antímilos, Khristianí SW of Santoríni, Tínos, Míkonos and Amorgós (SFENTHOURAKIS 1995).

Schizidium oertzenii (Budde-Lund, 1896) (syn. *Armadillidium o.*): Greece, central and southeastern Aegen islands SE of a line Ikaría–Sérifos, but missing on Crete (SCHMALFUSS 2005).

Schizidium tinum Sfenthourakis, 1995: Greece, Cyclades Islands, Tínos (SFENTHOURAKIS 1995).

Schizidium schmalfussi Sfenthourakis, 1992: Greece, Aegean island Día N of central Crete (SCHMALFUSS 2005).

Schizidium perplexum (Vandel, 1958) (syn. *Cretodillium p.*): Greece, eastern Crete (SCHMALFUSS 2005).

Schizidium beroni Schmalfuss, 2005: Greece, Aegean island Santoríni (SCHMALFUSS 2005).

Schizidium paragamiani Schmalfuss, 2005: Greece, central eastern Aegean, island Fúrni (SCHMALFUSS 2005).

Schizidium osellai Schmalfuss, 1988: Western Turkey, Manisa District, Boz Dağ, above 1300 m (SCHMALFUSS 1988).

Schizidium reinoehli Schmalfuss, 1988: Western and northwestern Turkey, N of Denizli and near Bolu (SCHMALFUSS 1988).

Schizidium fissum (Budde-Lund, 1885) (syn. *Armadillidium f.*, *bifidum*): Cyprus; southern Turkey along Gulf of Iskenderun; Lebanon (SCHMALFUSS 1988).

Schizidium festae (Dollfus, 1884) (syn. *Armadillidium f.*): Lebanon (SCHMALFUSS 1988).

Schizidium tiberianum Verhoeff, 1923: Northern Israel (SCHMALFUSS 1988, 1990).

Schizidium davidi (Dollfus, 1887) (syn. *Armadillidium d.*, *Pareluma minuta*, *S. minutum*, *S. kalalae*, *Armadillidium euphrati*): Iraq, Azerbaijan (SCHMALFUSS 1988).

Schizidium rausi Schmalfuss, 1988: Southeastern Turkey, Lake of Van (SCHMALFUSS 1988).

Schizidium golovatchi Schmalfuss, 1988: Armenia (SCHMALFUSS 1988).

Schizidium persicum Schmalfuss, 1986: Northern Iran (SCHMALFUSS 1986).

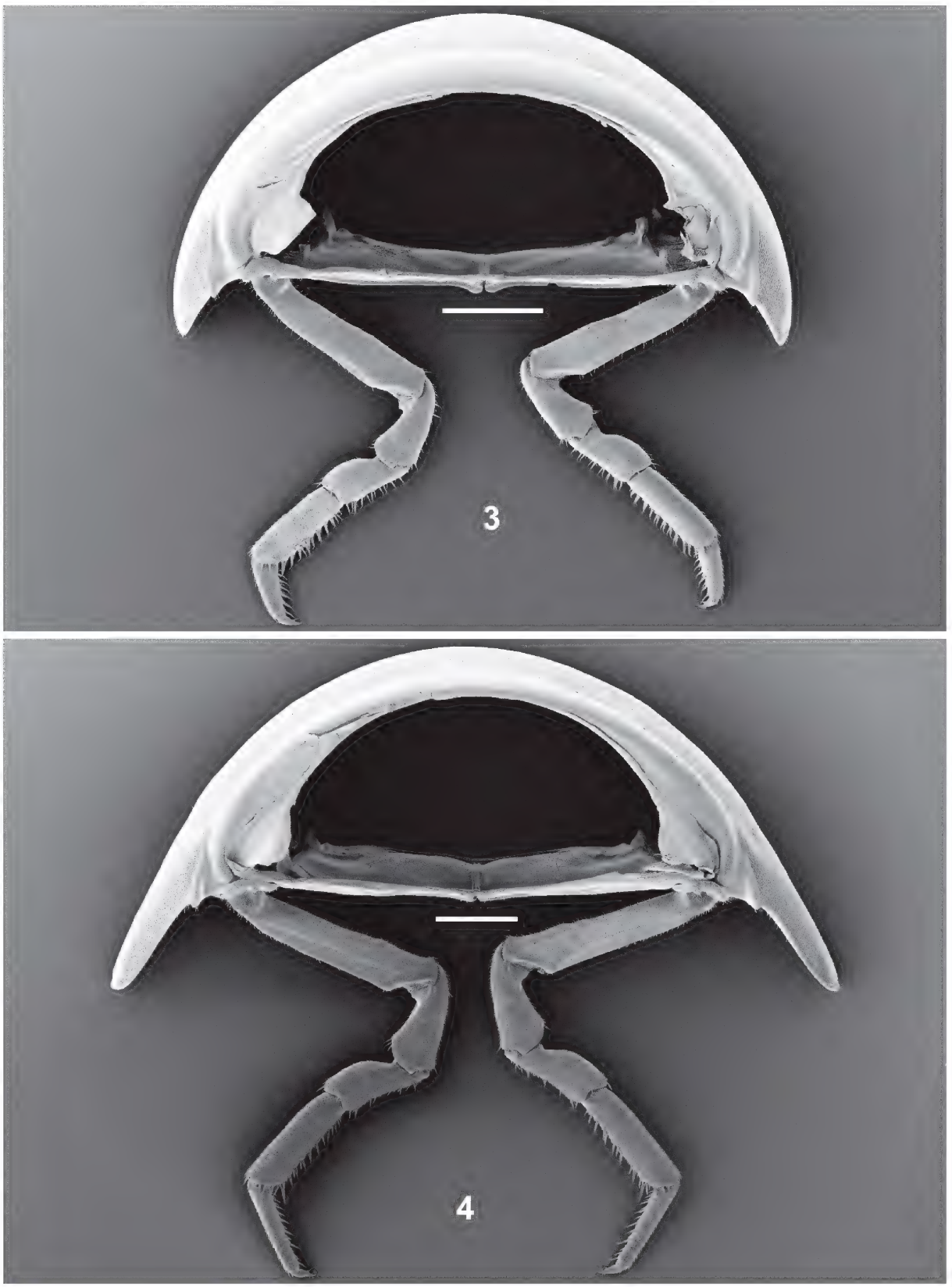
4 Distribution and ecology

The genus *Schizidium* in the definition given above is distributed from Greece to Iran (Fig. 1). In Greece it populates most central and southern Aegean islands, west and north of that region three isolated populations have been discovered (Fig. 2). One has been found on a small island of the Northern Sporades (*S. graecum*), one on the east-central mainland in Attica (*S. atticum*) and one on the northwestern Peloponnese (*S.* n. sp., undescribed). It is tempting to interpret these three populations as relicts of a formerly more continuous distribution on the Greek mainland. Possibly the pluvial periods during the Ice Age have led to a recent immigration of competitors and predators which were formerly missing on the southern Greek mainland. The isopod genus *Armadillidium* Brandt, 1833 could be one of the competing groups. It seems that several clades of that genus have invaded the Peloponnese in recent geological times from the north, which led to a small radiation resulting in 18 species nowadays populating the Peloponnese (SCHMALFUSS 2006). This could have, in combination with changes of climate, vegetation and predator spectrum, led to the extinction of the epigean guild of the *Schizidium* species. The three relict populations found up to now are all pigmentless endogean species with reduced eyes.

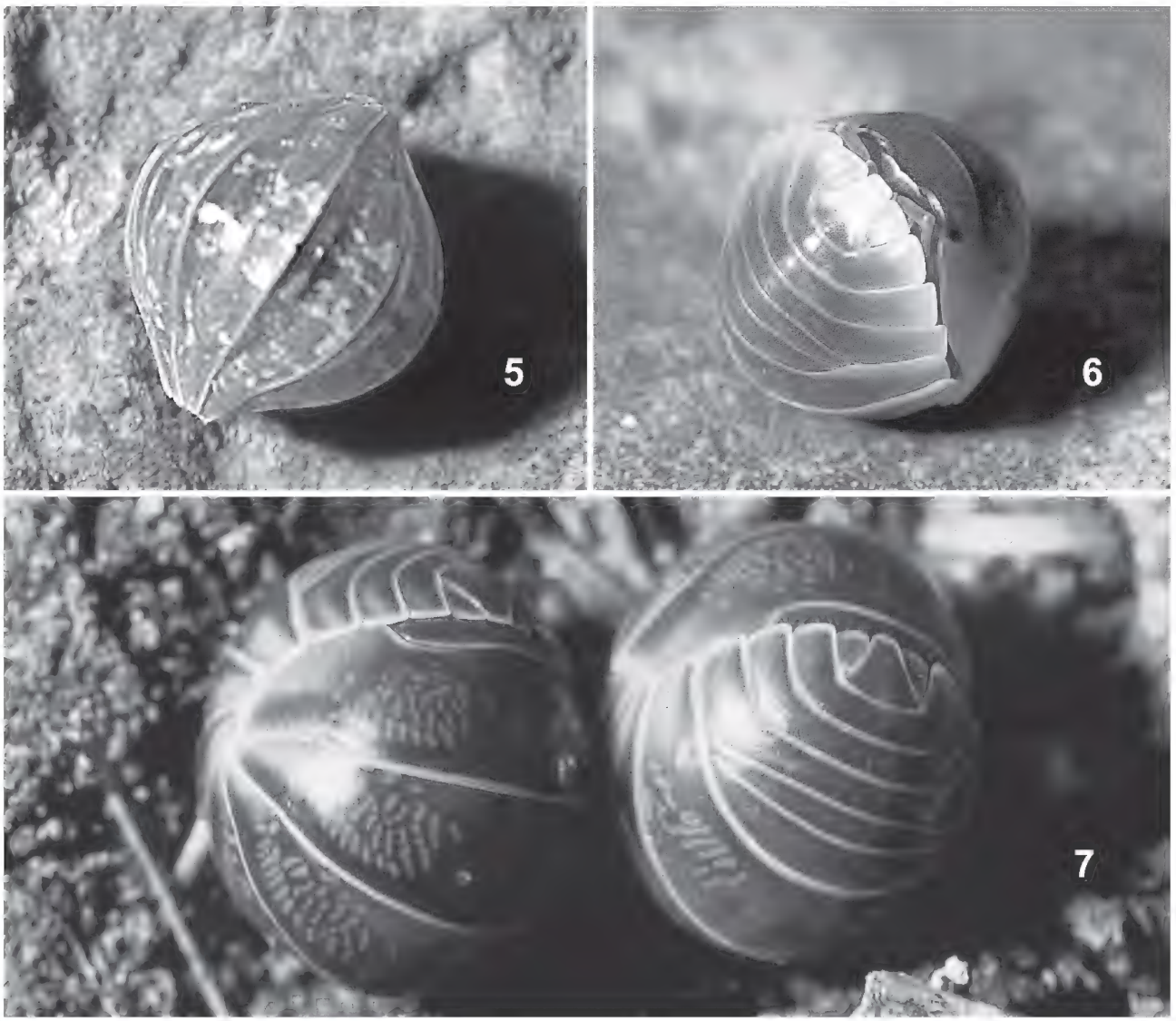
On the Aegean islands three eco-morphological types of *Schizidium* species are present:

- Fully pigmented forms living an epigean way of life, hiding in daytime under stones and moving around on the soil surface in the night (*S. hybridum*, *S. oertzenii* and *S. schmalfussi*).
- Endogean species without or with reduced pigmentation and eyes, small-sized, living in crevice-systems of stony soils and normally not moving around on the open surface.
- Cave species, without pigmentation and with reduced or missing eyes, medium-sized, living in limestone cave systems (*S. perplexum* on eastern Crete and *S. beroni* on the island of Santoríni).

The fully pigmented epigean species live in open dry maquis and phrygana biotopes, where the genus *Armadillidium* occurs only with very few species, which are additionally fixed to the sea coast. On the island of Ródos *Schizidium oertzenii* is the most numerous and the biggest terrestrial isopod species – rolled-up animals reach the size of small cherries – while the three species of *Armadillidium* (*A. ameglioi* Arcangeli, 1914, *A. granulatum* Brandt, 1833 and *A. marmoratum* Strouhal, 1929, with *A. vulgare* (Latreille, 1804) missing completely on the island) are only found close to the sea-side.



Figs. 3–4. Frontal view of 3rd pereionite. – **3**. *Schizidium oertzenii*. **4**. *Armadillidium* sp. (undescribed species from northeastern Greece). – Scales: 1 mm.

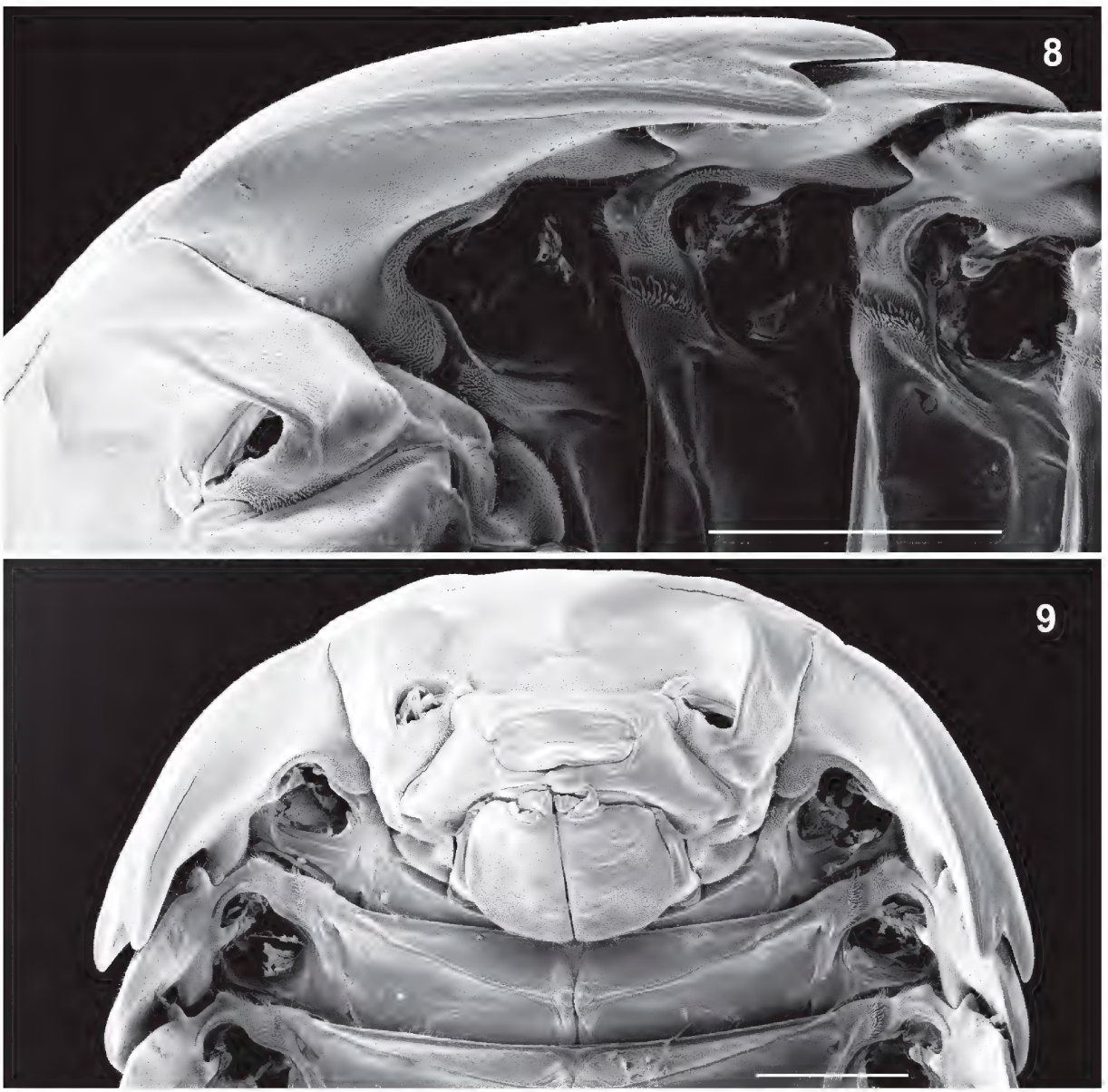


Figs. 5–7. Rolled up animals. – **5**. *Armadillidium ameglioi* Arcangeli, 1914 (Greece: Ródos Island), rolled up to a lemon-shaped ball. **6**. *Armadillidium* sp. (as Fig. 4), leaving fissures for a possible insertion of pointed appendages to inject poison into vulnerable ventral parts. **7**. *Schizidium oertzenii* (Greece: Ródos Island) rolled up to a smooth, perfectly closed "euspheric" ball.

The *Schizidium* species known up to now from western Asia are all pigmented epigean forms living in dry Mediterranean biotopes, but never venturing into semi-deserts or deserts. One species, *S. persicum*, has been found on the Elburs Mountains (northern Iran) in deciduous forest; the genus *Armadillidium* is not present in that region.

5 Morphological adaptations

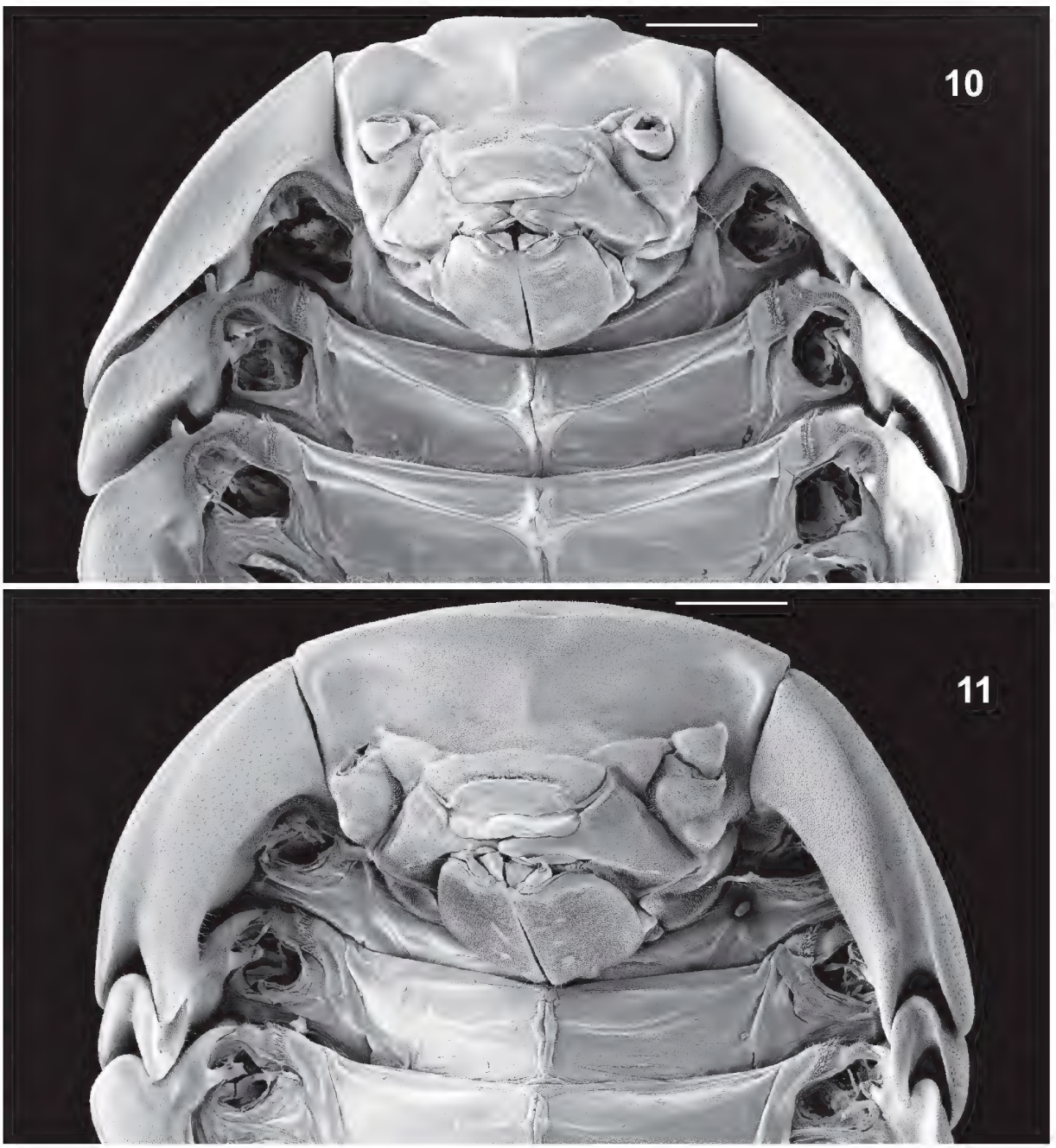
All species of *Schizidium* are able to roll up to a completely closed ball. The cross-sections of the pereion-tergites are semi-circular (Fig. 3), so the rolled-up animal is completely round ("euspheric" conglobation). This and the fact that the tergite surface is completely smooth leads to an effect which I call "flick-away principle". If any predator tries to get hold of the rolled-up animal with a pincer-like instrument (bird's bill, scorpion's pedipalp, even the jaws of lizards and small mammals) there is a good chance of the animal sliding away and rolling into some crevice where it is out of the reach of the predator. This flick-away principle applies for all euspheric isopods with smooth tergal surfaces, as e. g. for *Armadillidium vulgare* (family Armadillidiidae) and *Armadillo officinalis* Duméril, 1816 (family Armadillidae). It does not apply for tuberculated



Figs. 8–9. *Schizidium oertzenii*. – **7**. Ventral view of lateral margin of pereion-tergite 1 with schisma, left side. **8**. Ventral view of anterior pereionites. – Scales: 1 mm.

species as *Armadillo tuberculatus* Vogl, 1876 (family Armadillidae) and for species with flat epimera which roll up into a lemon-shaped structure ("pseudospheric" conglobation as in many species of *Armadillidium*, see Figs. 4, 5). The walking legs are always sheltered inside the ball, so the pseudospheric species with flatter epimera and thus a wider diameter of the pereionites can have longer legs allowing for a more rapid locomotion. The strategy to minimize predation is in this case rather to run away than to rely on the flick-away principle.

The *Schizidium* species have developed further morphological adaptations to form a completely closed ball. In the rolled-up animal the posterior parts of the abdomen are tightly covering the frontal edge of the 1st tergite and the frontal part of the head (Fig. 7). Additionally the inner side of the hind edge of the first pereion-tergite bears a process which leads to formation of a groove ("schisma", Figs. 8, 9) at the hind corner of the epimeron. In the rolled-up animal the margin of the 6th pereion-tergite is positioned in this groove, which prevents an



Figs. 10–11. Ventral view of anterior pereionites. – **10**. *Armadillidium vulgare* (Latreille, 1804). **11**. *Armadillo officinalis* Duméril, 1816. – Scales: 1 mm.

opening of the ball by shearing forces. All this results in a perfect closure of the ball, and no fissure is left that can be used by a predator to insert a pointed appendage and to inject poison into the vulnerable ventral parts (spiders, scorpions, chilopods). So this strategy seems to be directed especially against arthropod predators that overwhelm their prey by injecting venoms. In *Armadillidium* the rolled-up animal cannot be closed without leaving fissures that can be used for poisonous injections (Fig. 6), and the schisma is missing (Fig. 10), thus a predator can open the ball by shearing forces and get access to the vulnerable ventral parts. The genus *Armadillo* possesses a schisma at the hind corner of the first epimeron which continues as a groove to the frontal corner (Fig. 11) and even on the frontal part of the head (Fig. 12). In the rolled-up animal the margins of the 6th and 7th pereion-

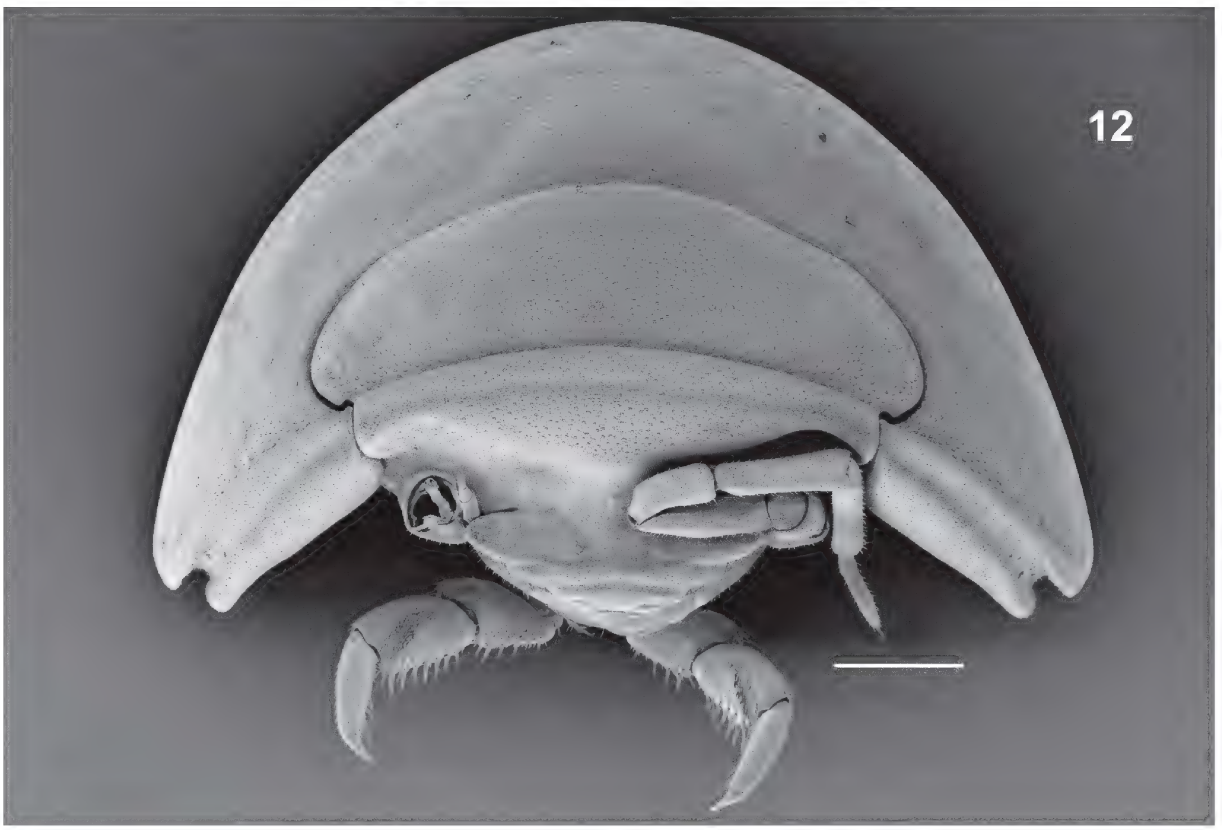


Fig. 12. *Armadillo officinalis*, frontal view of head and pereion-tergite 1. Note continuation of epimeral grooves on frontal part of head. – Scale: 1 mm.

tergites fit into this groove, so the animal is secured against shearing forces, and the posterior margins of the pleon-epimera and the telson are tightly pressed against the depression on the frontal margin of the head. In this way, as it is the case in *Schizidium*, the rolled-up animal does not offer any fissures for pointed appendages to get access to the vulnerable ventral parts.

The *Schizidium* species populate the eastern Mediterranean region and the Middle East countries north of the desert belt, where they live in open dry maquis and phrygana biotopes. Considering their morphological adaptations which have obviously been acquired to minimize predation, it seems that in these biotopes the crucial part of the predator spectrum consists of arthropods. This would mean selective advantages over competitors like *Armadillidium*, and it would explain the present-day distribution of *Schizidium*. On the other hand – contrasting the Greek mainland with the southern Aegean islands – other segments of the predator spectrum, e. g. mammals, should dominate in the continental biotopes with denser and higher vegetation. Shrews for instance, practically lacking on the islands, certainly could take a heavy toll on prey like isopods. In these biotopes – as far as the Greek region is concerned – *Armadillidium* is obviously the better adapted group of the conglobating isopods. The genus *Armadillo*, with morphological anti-predation strategies similar to those of *Schizidium*, is present with two species in the Aegean region (one only on the islands). In the Near East it penetrates into semi-desert and desert biotopes, where it has differentiated into a dozen different species (Schmalfuss 1996).

6 Conclusions

In the "rollers" among terrestrial isopods different types of morphological adaptations exist. The three genera *Armadillidium*, *Schizidium* and *Armadillo* are the dominating conglobating groups in the eastern Mediterranean region. Each of these genera exhibits a different set of characters to perform the rolling-up behavior. The different strategies obviously lead to different survival values in the biotopes prevailing in the treated region. *Armadillidium* seems to have advantages in continental biotopes with dense and highly developed vegetation, *Schizidium* is the dominant group in open dry maquis and phrygana

biotopes, and *Armadillo* has its highest species numbers and population densities under semi-desert conditions.

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Manuscript received: 20.XII.2006, accepted: 16.III.2007.

The terrestrial isopods (Isopoda: Oniscidea) of Greece. 25th contribution: The genus *Armadillidium* (Armadillidiidae) in the provinces Macedonia and Thrace[1]

Helmut Schmalfuss

Abstract

Based on the investigation of new collections, 14 species of *Armadillidium* are reported from the northern mainland of Greece (provinces of Macedonia and Thrace). Seven species are new to science (*A. jerrentrupi* **n. sp.**, *A. pangaionum* **n. sp.**, *A. petralonense* **n. sp.**, *A. phalacronum* **n. sp.**, *A. pieperi* **n. sp.**, *A. sfenthourakisi* **n. sp.** and *A. tuberculatum* **n. sp.**). Four species were treated in previous contributions of this series. The diagnostic characters of ten species (including the seven new ones) are described and illustrated, most of them by SEM-photographs, and the Greek records of these species are mapped.

Keywords: Isopoda, Oniscidea, *Armadillidium*, northern Greece.

Zusammenfassung

Die Untersuchung neuer Aufsammlungen ergab 14 *Armadillidium*-Arten auf dem nordgriechischen Festland (Provinzen Makedonien und Thrakien). Sieben dieser Arten sind neu für die Wissenschaft (*A. jerrentrupi* **n. sp.**, *A. pangaionum* **n. sp.**, *A. petralonense* **n. sp.**, *A. phalacronum* **n. sp.**, *A. pieperi* **n. sp.**, *A. sfenthourakisi* **n. sp.** und *A. tuberculatum* **n. sp.**). Vier Arten wurden in vorangehenden Beiträgen dieser Serie behandelt. Die diagnostischen Merkmale der sieben neuen und drei weiterer Arten werden beschrieben und illustriert, die meisten mit Hilfe von REM-Aufnahmen, und die griechischen Nachweise dieser Arten werden kartiert.

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1 Introduction

In the first part of this new revision of the Greek species of *Armadillidium* (Schmalfuss 2006a) the species from the Peloponnese were treated. Presently 18 species are known from the peninsula, six of them were described as new. The second part contains the species living on the Aegean islands (Schmalfuss 2006b). It comprises 13 species, none of which was new. Six of them also occur on the Peloponnese, so they were treated in the first part. The present third part is dedicated to the species of the northern Greek mainland, comprising the provinces of Macedonia and Thrace (Fig. 1). This region is, concerning isopods, obviously the most underinvestigated part of Greece, seven of the 14 *Armadillidium* species recorded from there are new to science. Four of the species have been treated in the previous two contributions, so descriptions, illustrations and maps are given for ten species. With the new

[1] 24th contribution see Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 698 (2006).

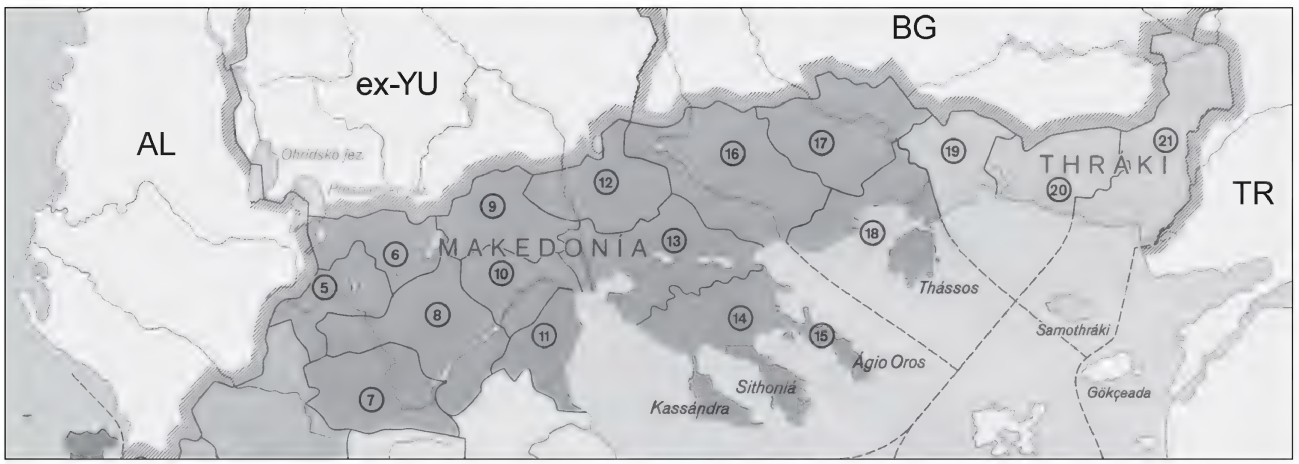


Fig. 1. Map of the treated area consisting of the northern Greek provinces Macedonia and Thrace. – The numbers indicate the political districts (nomoí) which are used to localize the collecting data: 5 = Kastoriá, 6 = Flórina, 7 = Grevená, 8 = Kozáni, 9 = Péla, 10 = Imathía, 11 = Pieriá, 12 = Kilkís, 13 = Thessaloníki, 14 = Khalkidikí, 15 = Ágio Óros, 16 = Sérres, 17 = Dráma, 18 = Kavála, 19 = Xánthi, 20 = Rodópi, 21 = Évros.

species described in the present publication the total sum of valid species described from Greece adds up to 57. This number will increase, because the material from the remaining regions of Greece contains more new species.

Abbreviations

A.	*Armadillidium*
AL	Albania
BG	Bulgaria
ex.	example(s), specimen(s)
ex-YU	former Yugoslavia
GR	Greece
SMNS	Staatliches Museum für Naturkunde Stuttgart
TR	Turkey

Acknowledgments

The following persons have donated isopod material used in this revision: Dr. B. Baehr [formerly Hoffmann] (South Brisbane/Australia), Dr. M. Baehr (Munich/Germany), D. Bartsch (SMNS), Dr. E.-G. Burmeister (Munich/Germany), Dr. F. Erhard (Enzklösterle/Germany), Dr. R. Grimm (Tübingen/Germany), S. Huber (Oberuhldingen/Germany), Dr. J. Kontschán (Budapest/Hungary), Prof. Dr. W. Kühnelt † (Vienna/Austria), Dr. H. Malicky (Lunz am See/Austria), Dr. C. Manicastri (Rome/Italy), Prof. Dr. J. Martens (Mainz/Germany), Dr. G. Osella (L'Aquila/Italy), Dr. H. Pieper (Kiel/Germany), A. & F. Riedel (Kalambáka/Greece), O. Runze (Kiel/Germany), Dr. W. Schawaller (SMNS), J. Schönfeld (Westum/Germany), Dr. S. Sfenthourakis (Pátra/Greece), Dr. G. Steinbrück (Tübingen/Germany).

Dr. K. Wolf-Schwenninger and S. Leidenroth (both SMNS) operated the scanning electron microscope, and J. Reibnitz and Dr. H.-P. Tschorsnig (both SMNS) edited the SEM-photographs and the maps.

Dr. S. Sfenthourakis (Pátra/Greece) and Dr. S. Taiti (Florence/Italy) made valuable suggestions to improve an earlier draft of the manuscript.

To all of them I wish to express my sincere thanks.

2 Methods

The material used for the SEM-preparations was, if not stated otherwise, air-dried. In some cases a critical point treatment was used. If the number of specimens was not very limited I tried to find "clean" material for the SEM-preparations and prepared several specimens to be able to choose the cleanest one for the publication. In some species where the number of specimens was very restricted (e. g. *A. pieperi*) I had to use material covered with mud-particles, which nevertheless shows the relevant characters. Ultrasound treatment did not help to clean mud-covered material. The mounted material was coated with a 20 nm Au/Pd layer and examined with an ISI-SS40 scanning electron microscope at 10 KV. Digital photographs were directly acquired by using DISS 5 (point electronic).

3 The genus *Armadillidium* in Macedonia and Thrace

3.1 *Armadillidium album* Dollfus, 1887 (Figs. 2–12, map Fig. 13)

Literature records

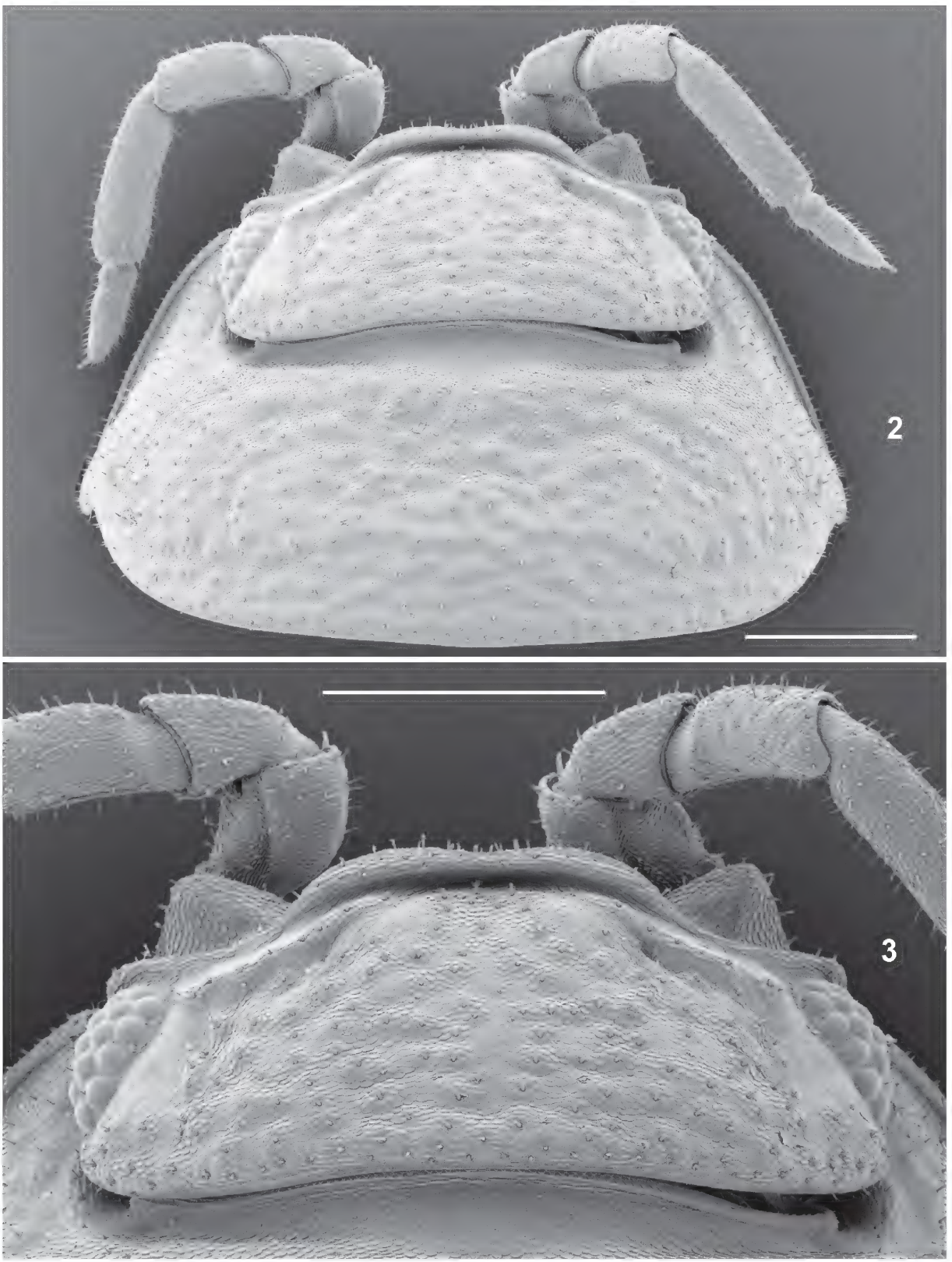
No literature records from Greece. A general treatment of the species is found in Vandel (1962: 841), a complete bibliographic list in Schmalfuss (2003: 27).

Material examined (including first records for Greece)

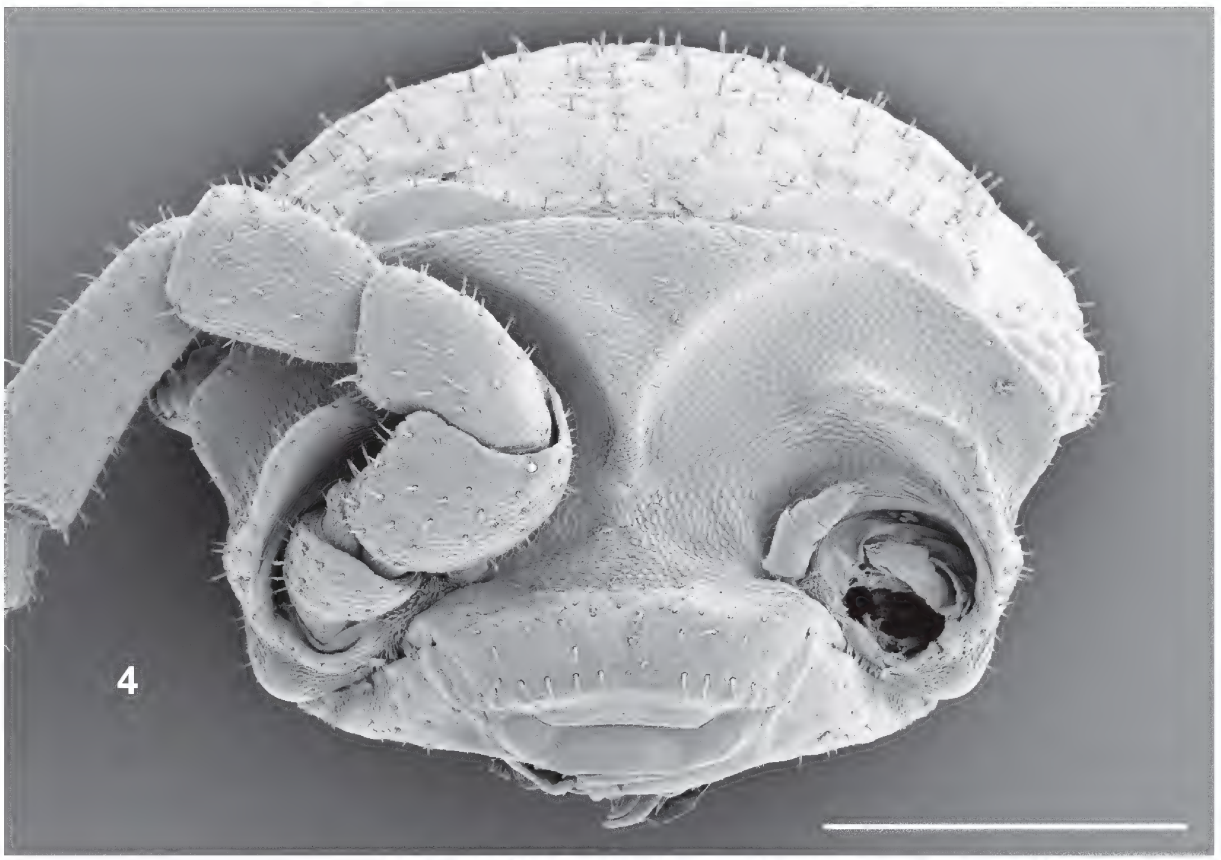
Greece: 15 ex., northeastern mainland, prefecture Rodópi, 7 km SW of Xilaganí, W of Ímeros harbor, sandy beach, under logs deeply buried in the sand, leg. Schmalfuss, 24.IV.1994 (SMNS 2421). – 1 ex., Ionian Islands, island Zákinthos, 10 km SE of Zákinthos, sandy beach, leg. Erhard, 15.V.1996 (SMNS 2576).

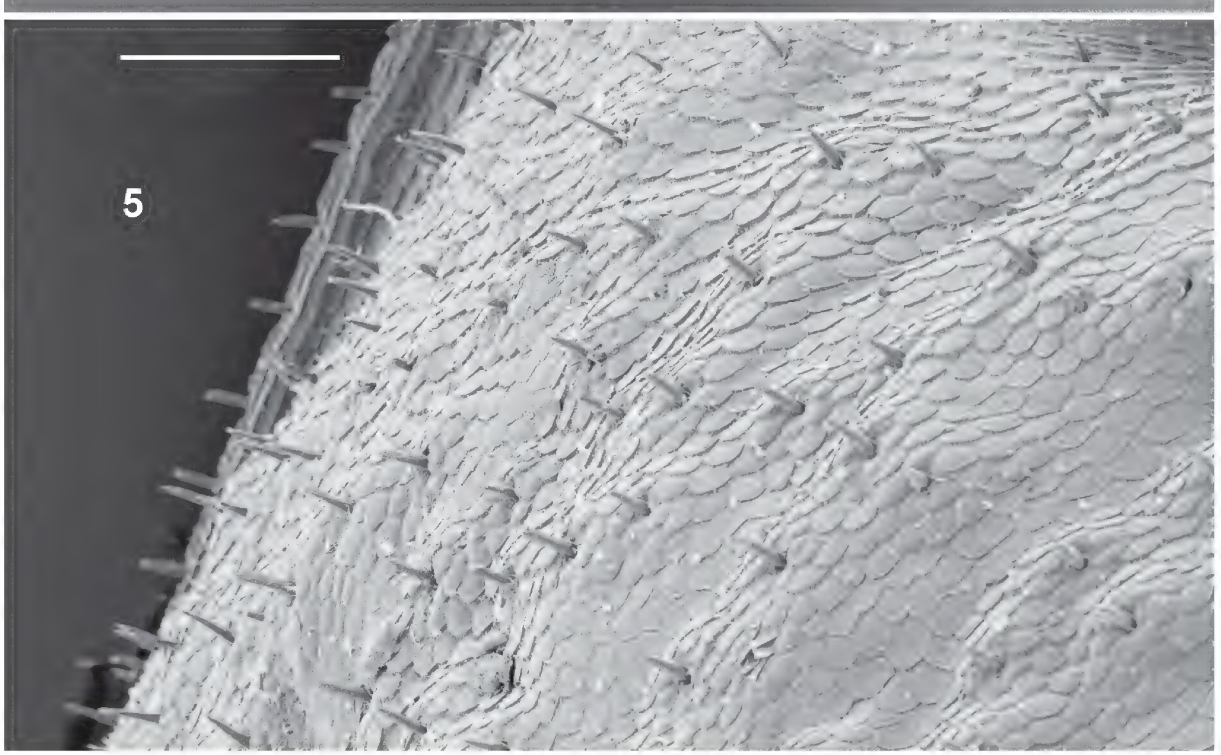
Italy: 1 ex., Sicily, Siracusa, Pantano Grande N of Pachino, leg. R. Grimm, 19.IV.1984 (SMNS 7218).

France: 2 ex., Mediterranean coast, S of Arles, Les Saintes

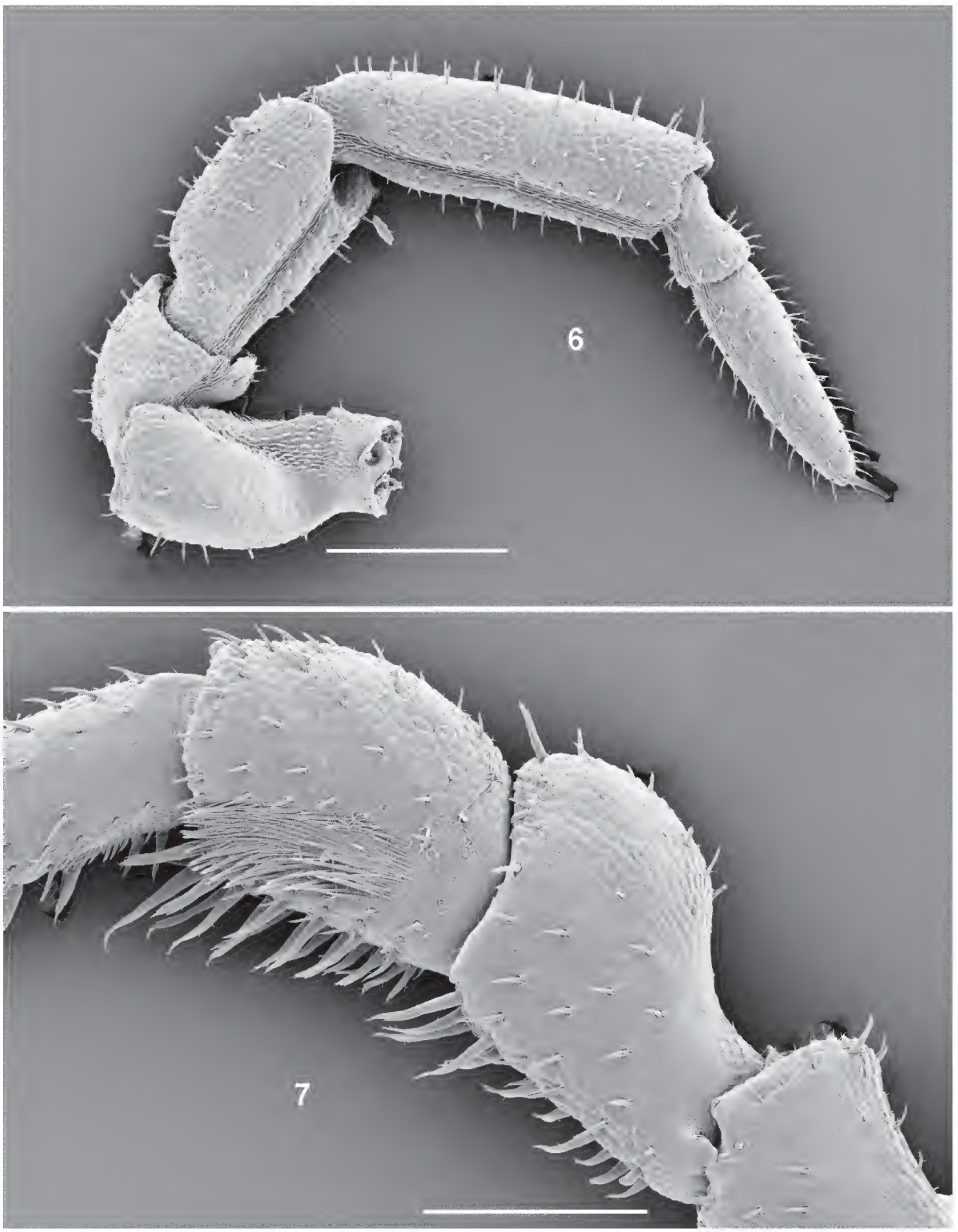


Figs. 2–3. *Armadillidium album* (northeastern Greece, SMNS 2421), ♀ with marsupium, 6.4 × 2.3 mm, critical point dried. – **2**. Head and pereion-tergite 1, dorsal view. **3**. Head, dorsal view. – Scales: 0.5 mm.

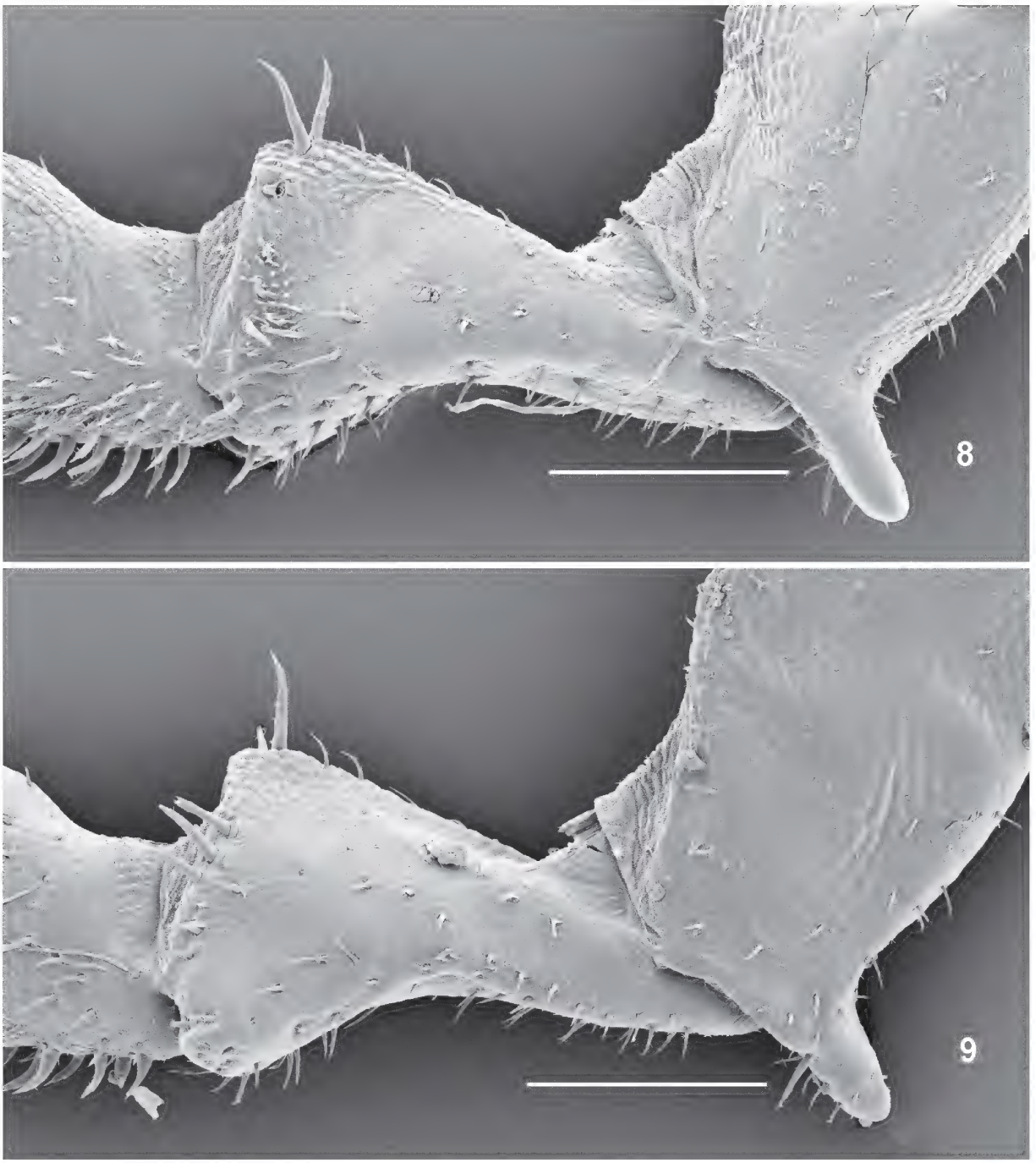




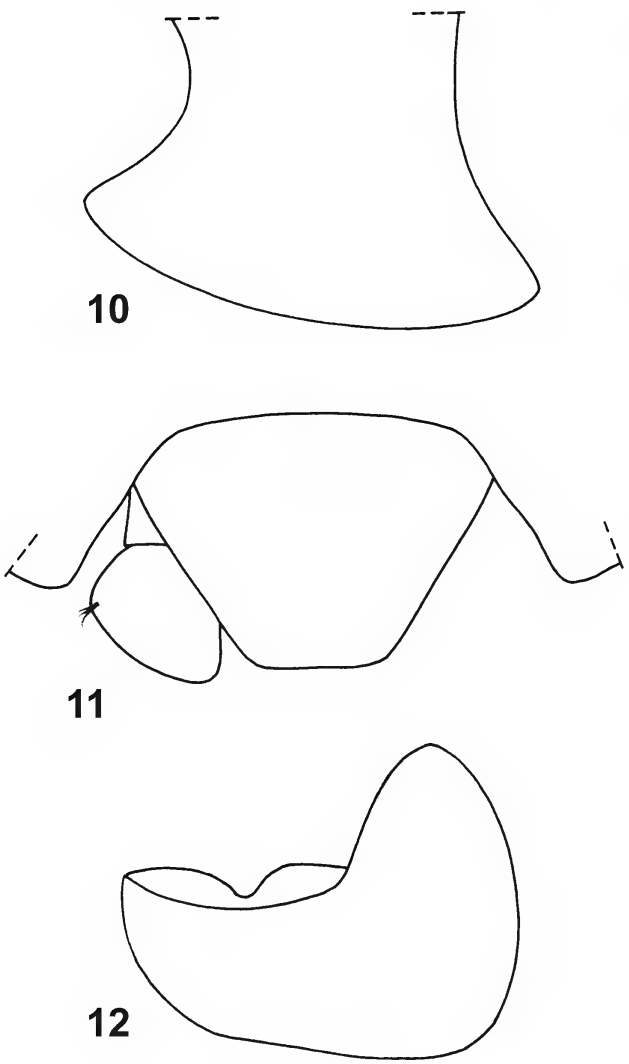
Figs. 4–5. *Armadillidium album* (northeastern Greece, SMNS 2421). – **4**. ♂, 5.2 × 2.0 mm, head, frontal view. **5**. ♀ with marsupium, 6.4 × 2.3 mm, critical point dried, detail of pereion-tergite 1. – Scales: 0.5 mm (4), 0.1 mm (5).



Figs. 6–7. *Armadillidium album* (northeastern Greece, SMNS 2421). – **6**. ♂, 4.4×1.7 mm, critical point dried, antenna. **7**. ♂, 5.2×2.0 mm, pereiopod 1, frontal view. – Scales: 0.2 mm.



Figs. 8–9. *Armadillidium album* (northeastern Greece, SMNS 2421), ♂, 5.2 × 2.0 mm. – **8**. Ischium 7, frontal view. **9**. Ischium 7, caudal view. – Scales: 0.2 mm.



Figs. 10–12. *Armadillidium album* (northeastern Greece, SMNS 2421). – **10**. ♀, 7.2 × 3.0 mm, pereion-epimeron 1, lateral view. **11**. ♀, 7.2 × 3.0 mm, telson and uropod, dorsal view. **12**. ♂, 5.5 × 2.3 mm, pleopod-exopodite 1, dorsal view.

Maries de la Mer, beach, leg. Burmeister, 20.V.1978 (SMNS 3063).

Spain: 1 ex., Mediterranean coast, province Gerona, Ampurias, leg. M. Baehr & B. Hoffmann, 10.IV.1981 (SMNS 9106). – 24 ex., Atlantic coast, Cantabria, Laredo, Oriñon, sandy beach, leg. Erhard, 3.I.1996 (SMNS 9316).

Madeira: 1 ex., Porto Santo, Ponta, leg. R. Grimm, 18.XII.1986 (SMNS 15365).

Tunisia: 1 ex., Nabeul, leg. Schönfeld, 16.IV.2001 (SMNS 15566).

Diagnostic characters

Maximum dimensions: 7.2 × 3.0 mm.

Coloration: Reduced pigmentation, yellowish with epimera partly light gray-brown.

Cuticular structures: Tergites slightly granulated, with short upright spiny setae (compare Fig. 5).

Head of duplocarinate type, with the ridge forming the upper edge of the frontal triangle extended to the sides of the head (Fig. 4) as in *A. bicurvatum* (Schmalfuss 2006a: 22, fig. 42). Frontal shield from behind surpassing frontal margin of head only slightly, upper margin straight, no angles laterally (Figs. 2–3); antennal lobes trapezoidal (Fig. 4). Hind margin of pereion-epimeron 1 completely rounded (Fig. 10). Telson shorter than wide, with straight sides and broadly truncated apex (Fig. 11). Antenna short and stout (Fig. 6), flagellum with distal segment about three times as long as proximal one. Male pereiopod 1 with brush of short spines on carpus and merus (Fig. 7); male pereiopod 7 with ischium ventrally concave, basipodite distally with very conspicuous process (Figs. 8–9). Male pleopod-exopodite 1 with rounded triangular hindlobe and indented respiratory field (Fig. 12), endopodite 1 with apex bent outwards.

Distribution

The species is known from the coast of the northern and southwestern Mediterranean (the present paper contains the first records from Greece, see map Fig. 13) and the Atlantic coasts of Europe north to England and the Netherlands. It has also been found on Madeira.

Remarks

In contrast to all other members of the genus the species lives in marine supra-littoral sandy beaches, where it is found on wooden logs and trunks deeply buried in the sand.

3.2 *Armadillidium bicurvatum* Verhoeff, 1901

This species was treated in the 23rd contribution of this series (Schmalfuss 2006a). It is known from the western parts of Greece including the Peloponnese and western Crete and has also been found in southern Albania.

3.3 *Armadillidium fossuligerum* Verhoeff, 1902 (Figs. 14–23, map Fig. 24)

Literature records (all from Greece)

Verhoeff 1902: 250 (Southern mainland, Timfristós Mountain); Verhoeff 1907: 484; Schmalfuss 1981: 283, figs. 35–41 (Timfristós Mountain); Schmalfuss 1985: 291 (Timfristós Mountain and Parnassós Mountain).

Material examined

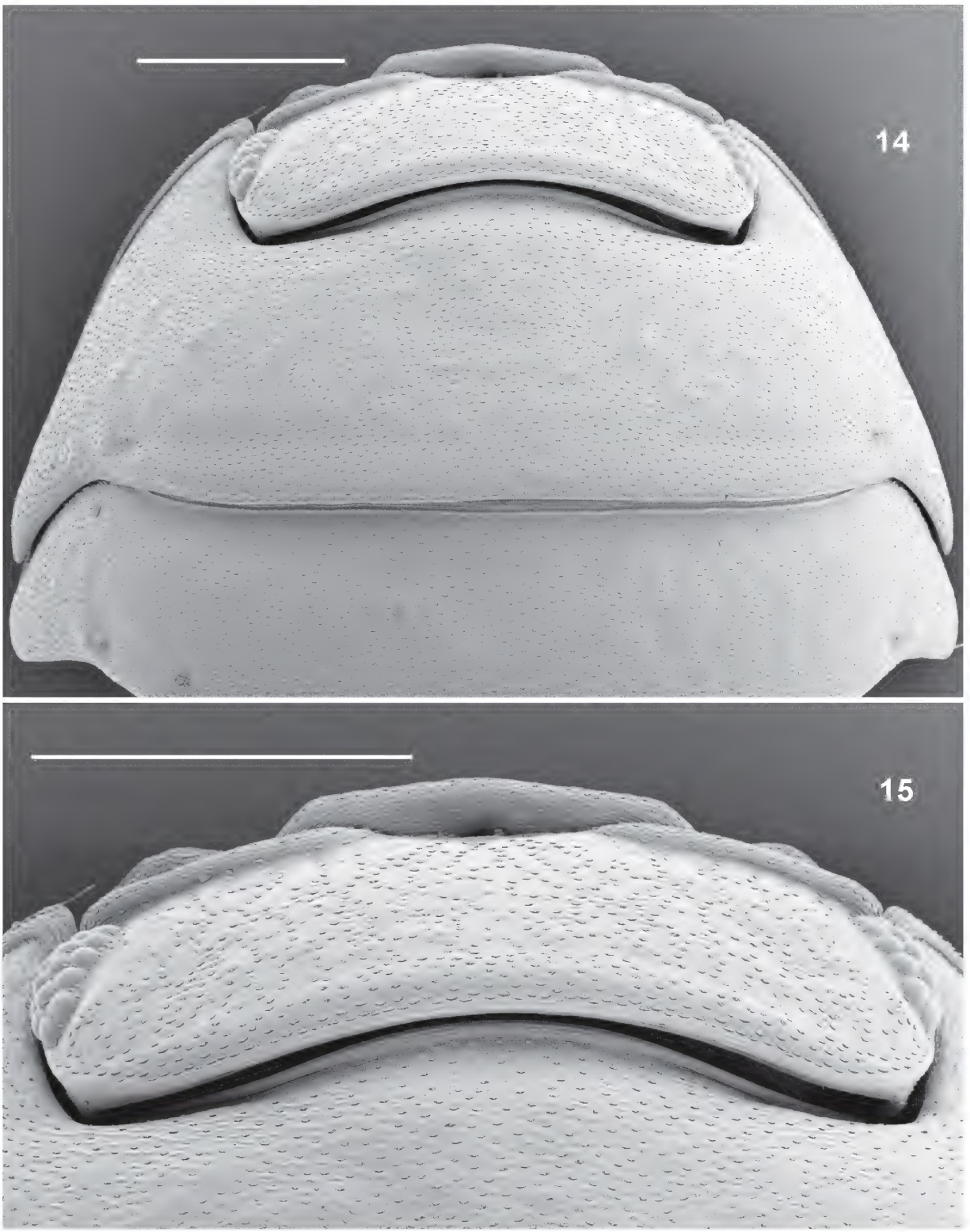
Greece: 8 ex., southern mainland, prefecture Viotía, Delfí, 400 m, leg. Bartsch, 30.VI.2005 (SMNS 2868). – 20 ex., as before, Parnassós Mountain, 1200–1800 m, leg. Malicky,

Fig. 13. Greek records of *Armadillidium album*.

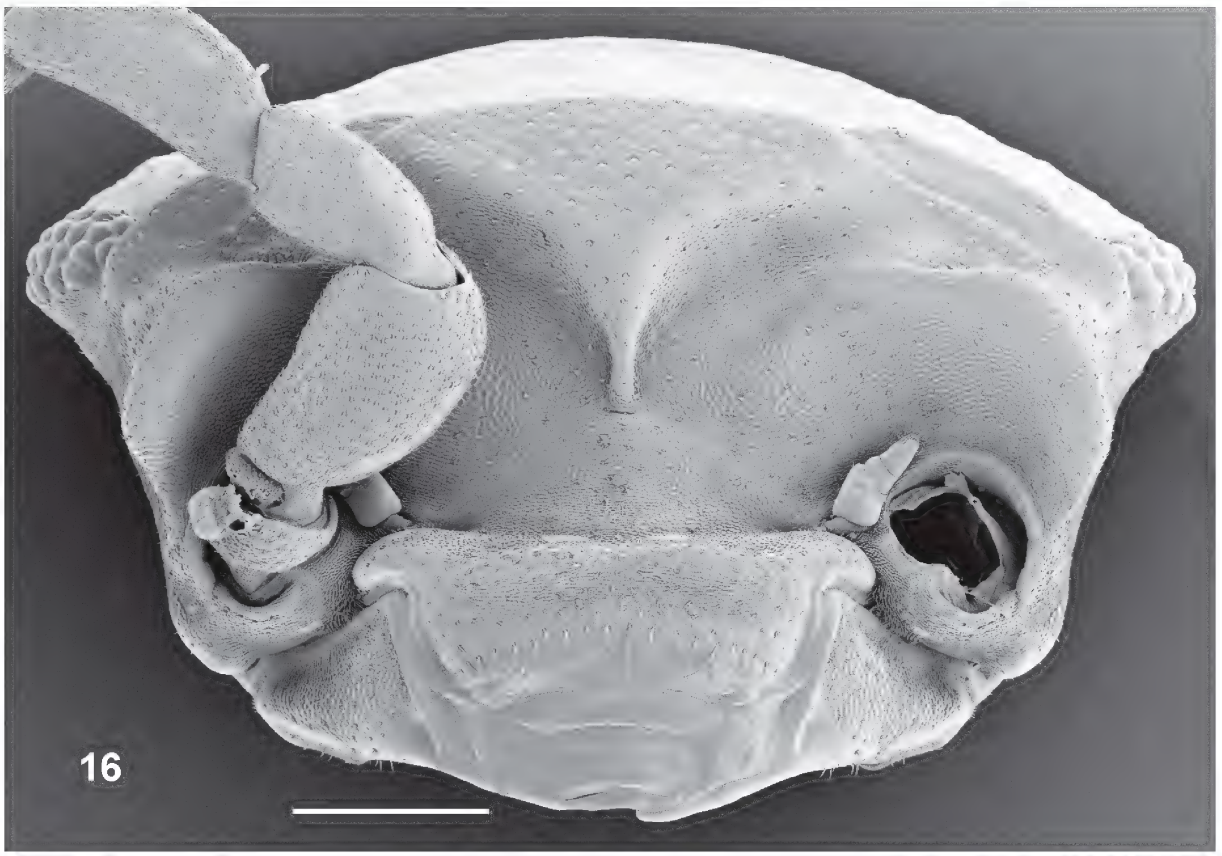
22.IV.1984 and leg. Schmalfuss, 11.X.2000 (SMNS 2101, 2680, 2681). – 1 ex., southern mainland, prefecture Etolía Akarnanía, Lake Trichonída, Pámfi, leg. Schmalfuss, 7.X.2000 (SMNS 2671). – 25 ex., southern mainland, prefecture Evritanía, Panetolikó Mountain, near Prussós, 1000–1200 m, *Abies*, leg. Malicky, 25.V.1987 and leg. Schmalfuss, 10.X.2000 (SMNS 2474, 2679). – 64 ex., as before, Timfristós Mountain, above Karpeníci, 1000–1600 m, *Abies*, leg. Schmalfuss, 28.–29.IX.1989 and 10.X.2000 (SMNS 2219, 2221, 2677, 2678). – 7 ex., central mainland, prefecture Tríkala, Kalambáka, Kastaniá, 1300–1500 m, leg. A. & F. Riedel, 26.V.2001 (SMNS 2705). – 23 ex., northern mainland, prefecture Imathía, Vérmio Mountain, 7 km SW of Véria, 600 m, maquis and deciduous forest, leg. Schawaller & Schmalfuss, 2.V.1994 (SMNS 2413). – 4 ex., northern mainland, prefecture Péla, Vérmio Mountain, 10 km S of Édessa, 500 m, deciduous forest, leg. Schmalfuss, 1.V.1994 (SMNS 2429). – 2 ex., northern mainland, prefecture Imathía, Piéria Mountains, Rizómata, leg. Pieper & Runze, 7.X.1978 (SMNS 1892). – 1 ex., northern mainland, Ólimpos Mountain, Fotiná, river shore with *Platanus*, leg. Schmalfuss, 30.IV.1979 (SMNS 1134). – 1 ex., top of Ólimpos Mountain, Skólio, leg. Kühnelt, 28.VII.1973 (SMNS 1809). – 4 ex., Ólimpos Mountain, between Pétra and Kokinopilós, leg. Runze, 10.V.1977 (SMNS 1772). – 1 ex., northern mainland, prefecture Thessaloníki, Lake Korónia, Evangelismós, leg. Schmalfuss, 14.V.1990 (SMNS 2264). – 3 ex., northern mainland, prefecture Sérres, Meníkio Mountain, Khionokhóri, 700 m, leg. Pieper, 11.V.2002 (SMNS 2745). – 2 ex., as before, Kerkíni Mountains, Áno Poría, 1000 m, leg. Steinbrück, 20.V.1988 (SMNS 2182). – 21 ex., as before, Kerkíni Mountains, above Platanákia, mixed forest, 500 m, leg. Schmalfuss, 13.V.1990 (SMNS 2258). – 18 ex., as before, Kerkíni Mountains, above Platanákia, *Fagus*, 800–1400 m, leg. Schmalfuss, 18.IX.1988 and 13.V.1990 (SMNS 2242, 2259, 2260). – 27 ex., as before, Lake Kerkíni, Lithótopos, leg. Steinbrück, 24.V.1988 and leg. Schmalfuss, 23.X.2005 (SMNS 2186, 2871, 2872).

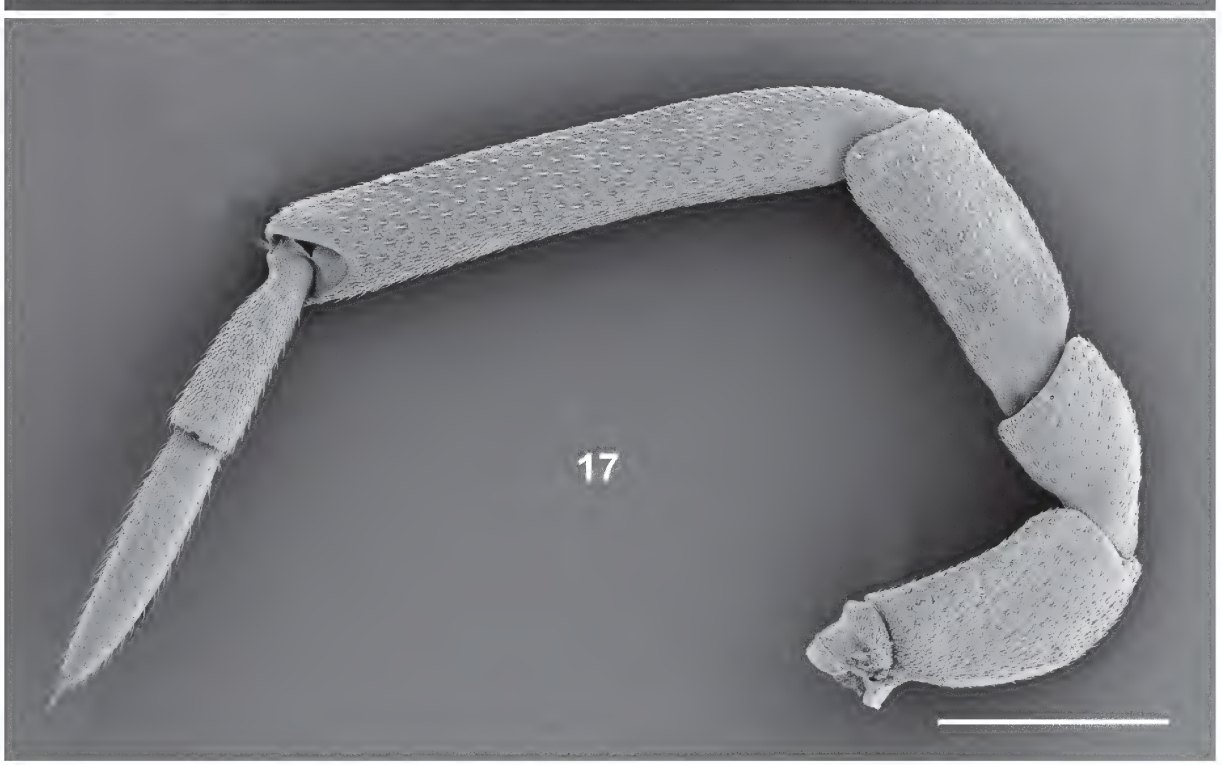
Ex-Yugoslavian Macedonia: 5 ex., southern part, river Vardar, Demir Kapija, leg. Kontschán et al., 17.X.2006 (SMNS 5059). – 9 ex., southeastern part, Belasica Mountains (continuation of the Kerkíni Mountains to the west), Kolešino, ruderal vegetation, 300 m, leg. Kontschán et al., 18.X.2006 (SMNS 5085).

Bulgaria: 11 ex., SW-Bulgaria, Pirin Mountains, 25 km S of

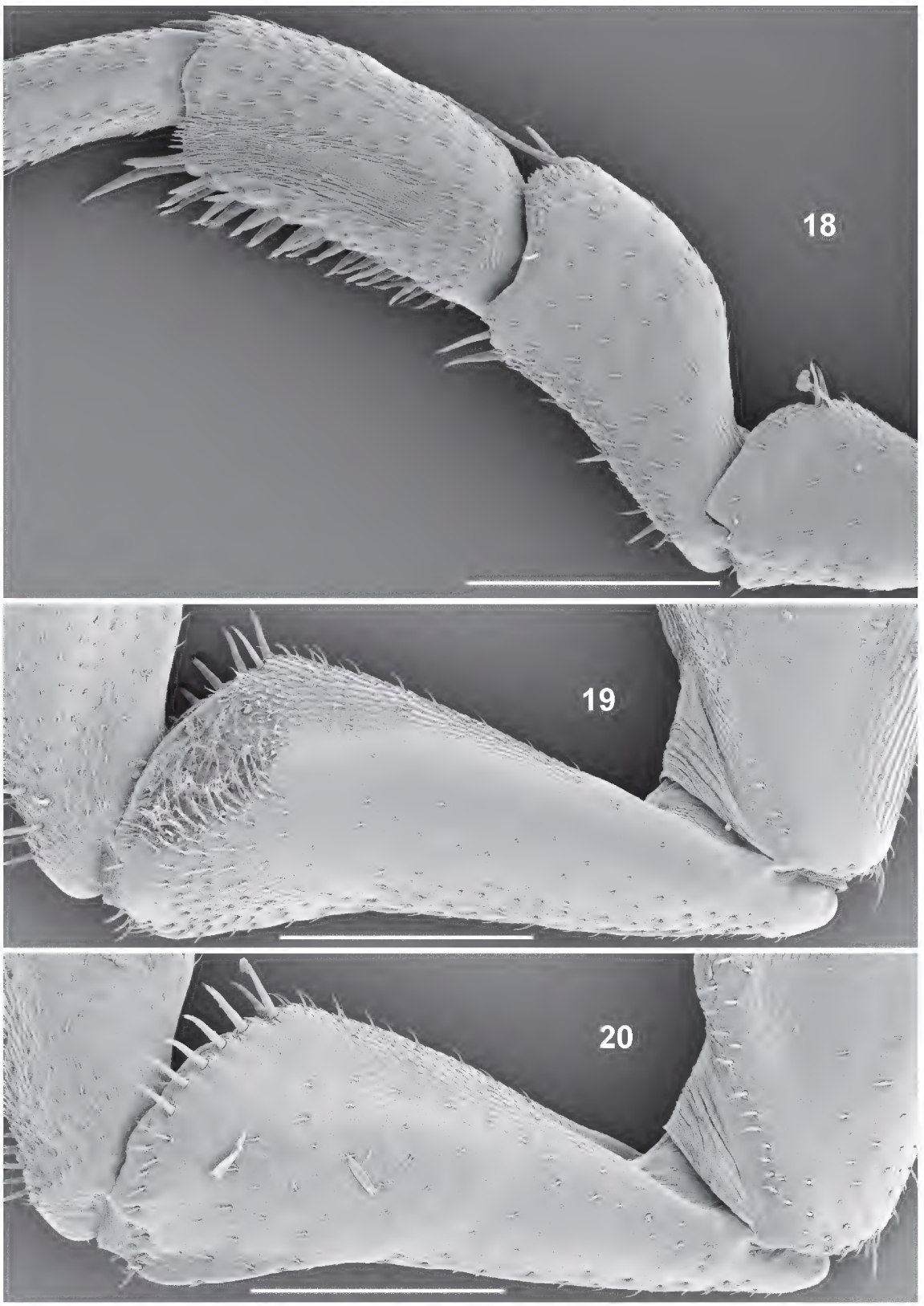


Figs. 14–15. *Armadillidium fossuligerum* (northern Greece, Vérmio Mountain, SMNS 2413), ♂, 11.5 × 4.5 mm. – **14**. Head and pereion-tergite 1, dorsal view. **15**. Head, dorsal view. – Scales: 1 mm.

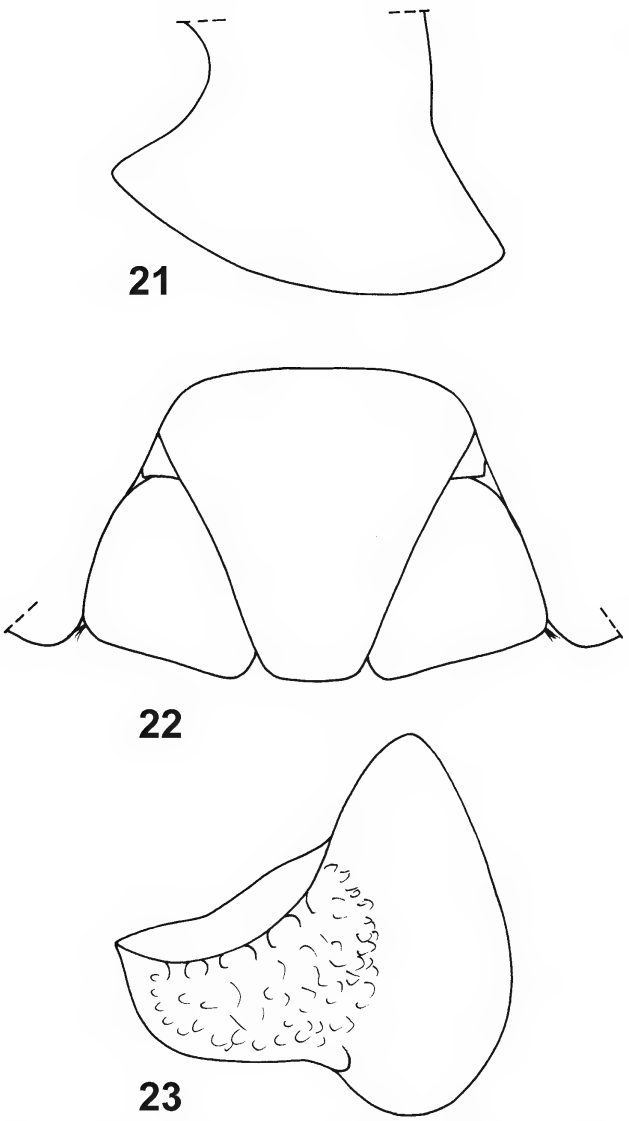




Figs. 16–17. *Armadillidium fossuligerum* (northern Greece, Vérmio Mountain, SMNS 2413). – **16**. ♀, 13.5 × 6.0 mm, head, frontal view. **17**. ♂, 11.5 × 4.5 mm, antenna. – Scales: 0.5 mm.



Figs. 18–20. *Armadillidium fossuligerum* (northern Greece, Vérmio Mountain, SMNS 2413), ♂, 11.5 × 4.5 mm. – **18**. Pereiopod 1, frontal view. **19**. Ischium 7, frontal view. **20**. Ischium 7, caudal view. – Scales: 0.4 mm.



Figs. 21–23. *Armadillidium fossuligerum* (northern Greece, Vérmio Mountain, SMNS 2413), ♂, 11.5 × 4.5 mm. – **21**. Pereion-epimeron 1, lateral view. **22**. Telson and uropods in situ, dorsal view. **23**. Pleopod-exopodite 1, dorsal view.

Blagoevgrad, 600 m, leg. S. Huber, 5.VIII.2005 (SMNS 5554). – 25 ex., SW-Bulgaria, N of Blagoevgrad, 550 m, leg. S. Huber, 6.VIII.2005 (SMNS 5558). – 17 ex., SW-Bulgaria, 30 km N of Blagoevgrad, Rila Monastery, edge of forest, 850 m, leg. S. Huber, 6.VIII.2005 (SMNS 5559).

Diagnostic characters

Maximum dimensions: 15 × 7 mm.

Coloration: Tergites grayish brown, epimera lighter, bigger specimens often uniformly blackish.

Cuticular structures: Variable, tergites smooth to granulated (Fig. 14). It seems that specimens from higher altitudes are less granulated.

Frontal shield from behind surpassing frontal margin of head in a varying degree, upper margin nearly straight to rounded, oblique angles laterally (Fig. 15); antennal lobes trapezoidal (Fig. 16). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 21). Telson as wide as long, with nearly straight sides and truncate apex (Fig. 22). Antenna see Fig. 17, distal segment of the flagellum slightly longer than proximal one. Male carpus 1 with brush of short spines (Fig. 18); male ischium 7 ventrally slightly concave, frontally with distal hair-field (Figs. 19–20). Male pleopod-exopodite 1 with triangular hind-lobe which can vary in length (Fig. 23), endopodite 1 with apex straight.

Distribution

Distributed in the mountain regions in southwestern Bulgaria, southeastern ex-Yugoslavian Macedonia and in a central belt through the Greek mainland (map Fig. 24).

Remarks

The species exhibits, according to its rather wide distribution, some morphological variation in the diagnostic characters, there is, however, no evidence for dividing it into different species.

3.4 *Armadillidium insulanum* Verhoeff, 1907

This species was treated in the 24th contribution of this series (Schmalfuss 2006b). It is known from the Aegean islands (except the Dodekánisa and Crete), the northeastern coast of Asia Minor and the northeastern mainland of Greece (map in Schmalfuss 2006b: 31, fig. 71).

3.5 *Armadillidium janinense* Verhoeff, 1902 (Figs. 25–33, map Fig. 34)

Synonym: *A. epirense* Strouhal, 1956.

Literature records (all from Greece)

Verhoeff 1902: 252 (Northwestern mainland, Ioánnina); Verhoeff 1930: 55, figs. 66–67; Strouhal 1956: 604, figs. 29–34 (*A. epirense*, northwestern mainland, province Ípiros, many localities); Schmalfuss 1981: 287, figs. 62–68; Schmalfuss 1985: 295, map fig. 13 (Northwestern mainland, prefectures Préveza, Thesprotía and Ioánnina); Sfenthourakis 1992: 159 (prefecture Ioánnina, Tímfi Mountain).

Material examined

Greece: 18 ex., southern mainland, prefecture Evritanía, Timfristós Mountain, above Karpenísi, 1500 m, *Abies*, leg. Schmalfuss, 28.IX.1989 (SMNS 2220). – 1 ex., northwestern mainland, province Ípiros, Voidomátis, leg. Sfenthourakis, 19.V.1990 (SMNS 2311). – 1 ex., northwestern mainland, prefecture Ioánnina, Anthokhóri SW of Métsovo, leg. Kühnelt,

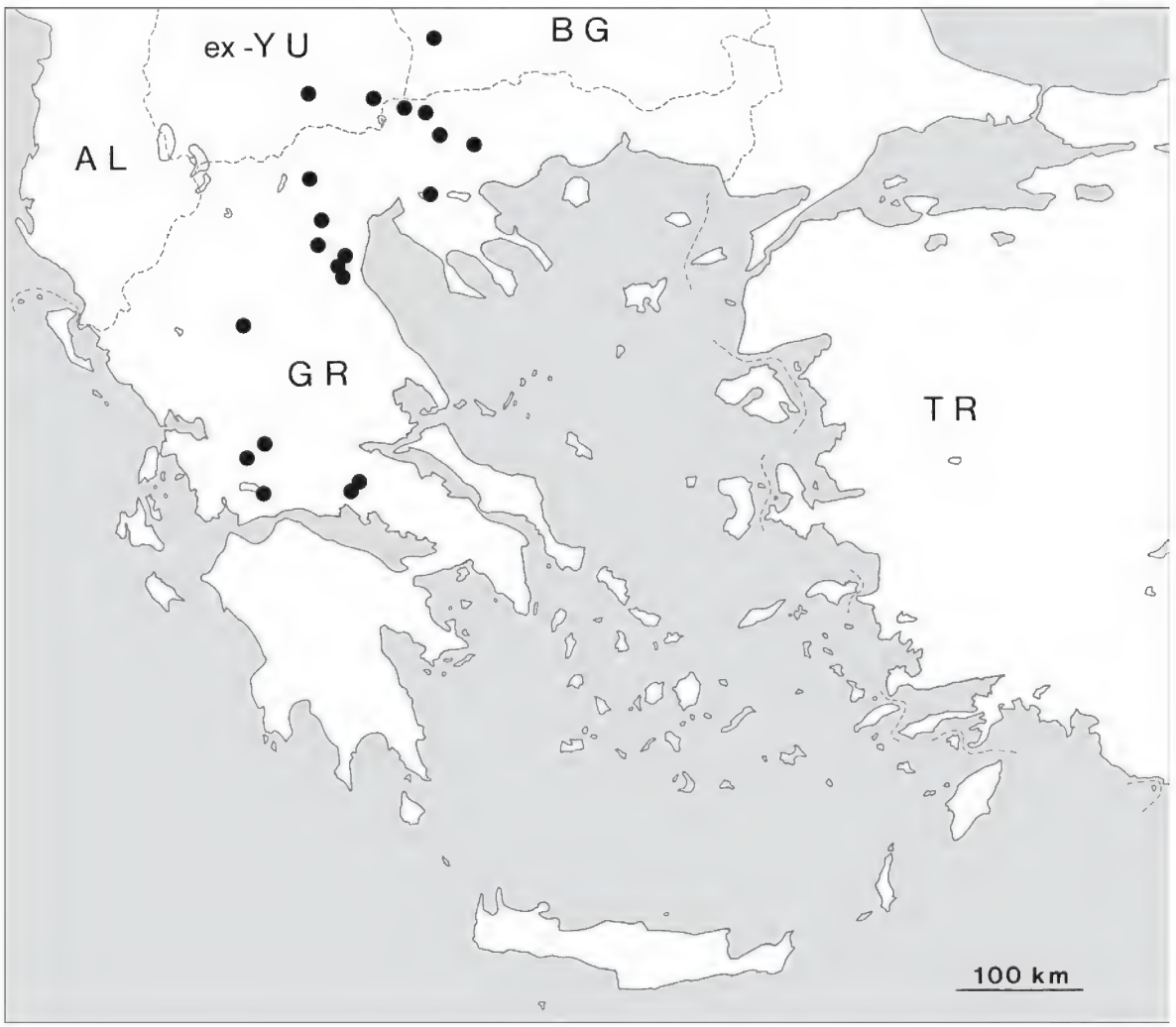


Fig. 24. Records of *Armadillidium fossuligerum*. Additional record from southwestern Bulgaria north of the area covered by the map.

15.VII.1968 (SMNS 1860). – 2 ex., prefecture Ioánnina, Métsovo, below Katára-Pass, 1300 m, *Fagus*, leg. Kontschán et al., 13.V.2006 (SMNS 1004). – 9 ex., prefecture Ioánnina, Tímfi Mountain, near Pápigko, 900 m, deciduous forest, leg. Sfenthourakis, 25.IX.1989 (SMNS 2751), leg. Schawaller & Schmalfuss, 5.V.1994 (SMNS 2411). – 1 ex., Tímfi Mountain, entrance to Víkos Gorge N of Arísti, 400 m, leg. Schmalfuss, 5.V.1994 (SMNS 2415). – 1 ex., Tímfi Mountain, Monodéndri, 1000–1500 m, leg. Bartsch, 21.VI.2005 (SMNS 2869). – 2 ex., northwestern mainland, prefecture Grevená, eastern part of Smólikas Mountain, Samarína, 1400 m, leg. Kontschán et al., 14.V.2006 (SMNS 1434).

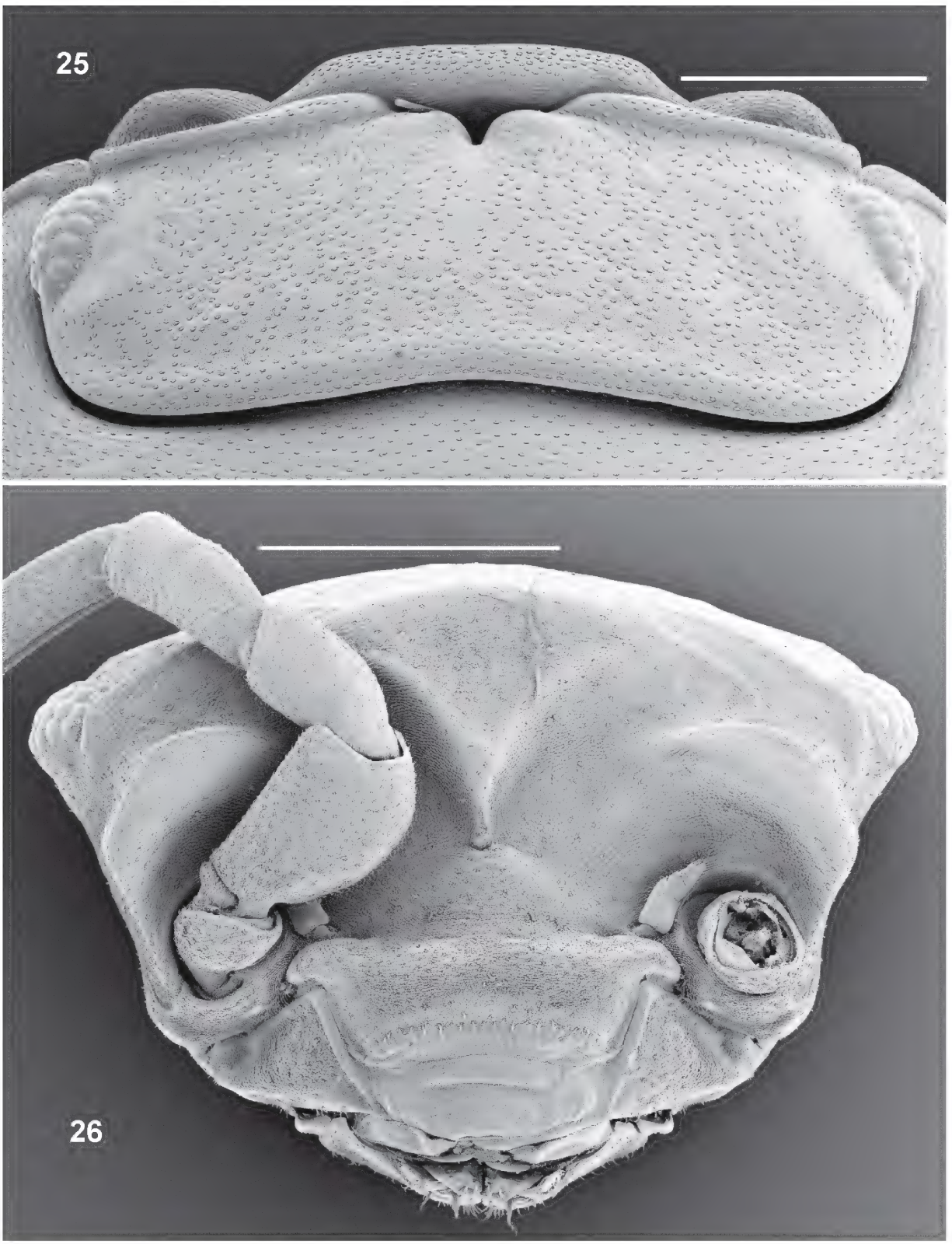
Diagnostic characters

Maximum dimensions: 16.0 × 7.7 mm.

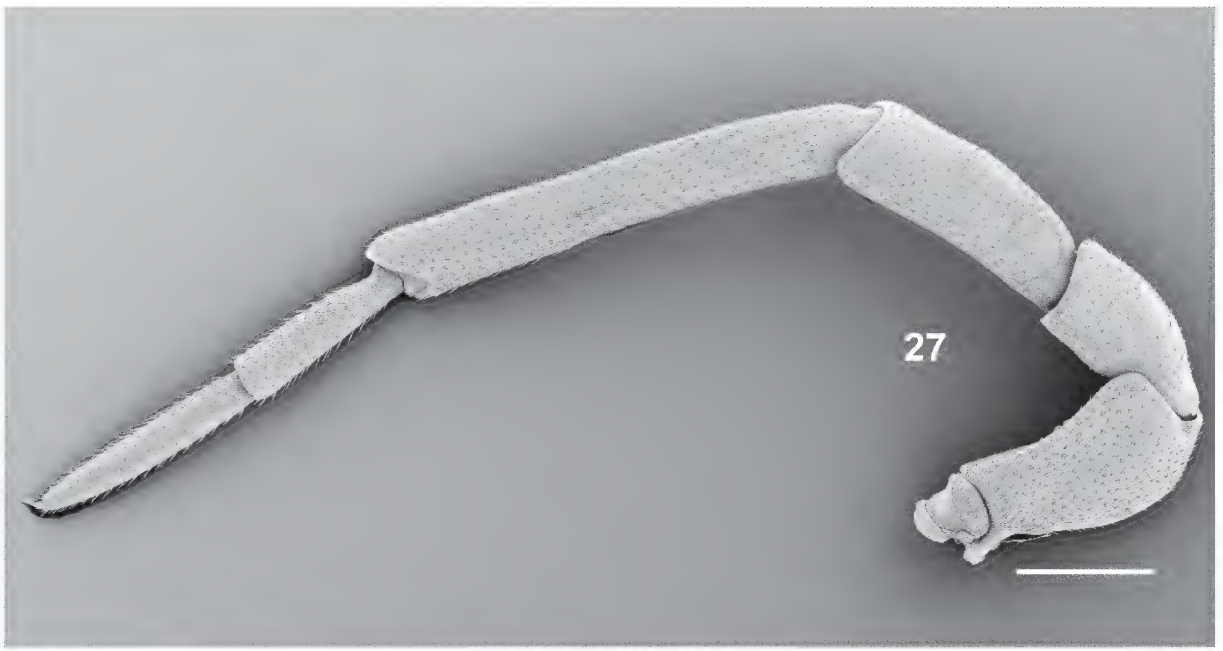
Coloration: Light brown with epimera lighter, big males uniformly blackish.

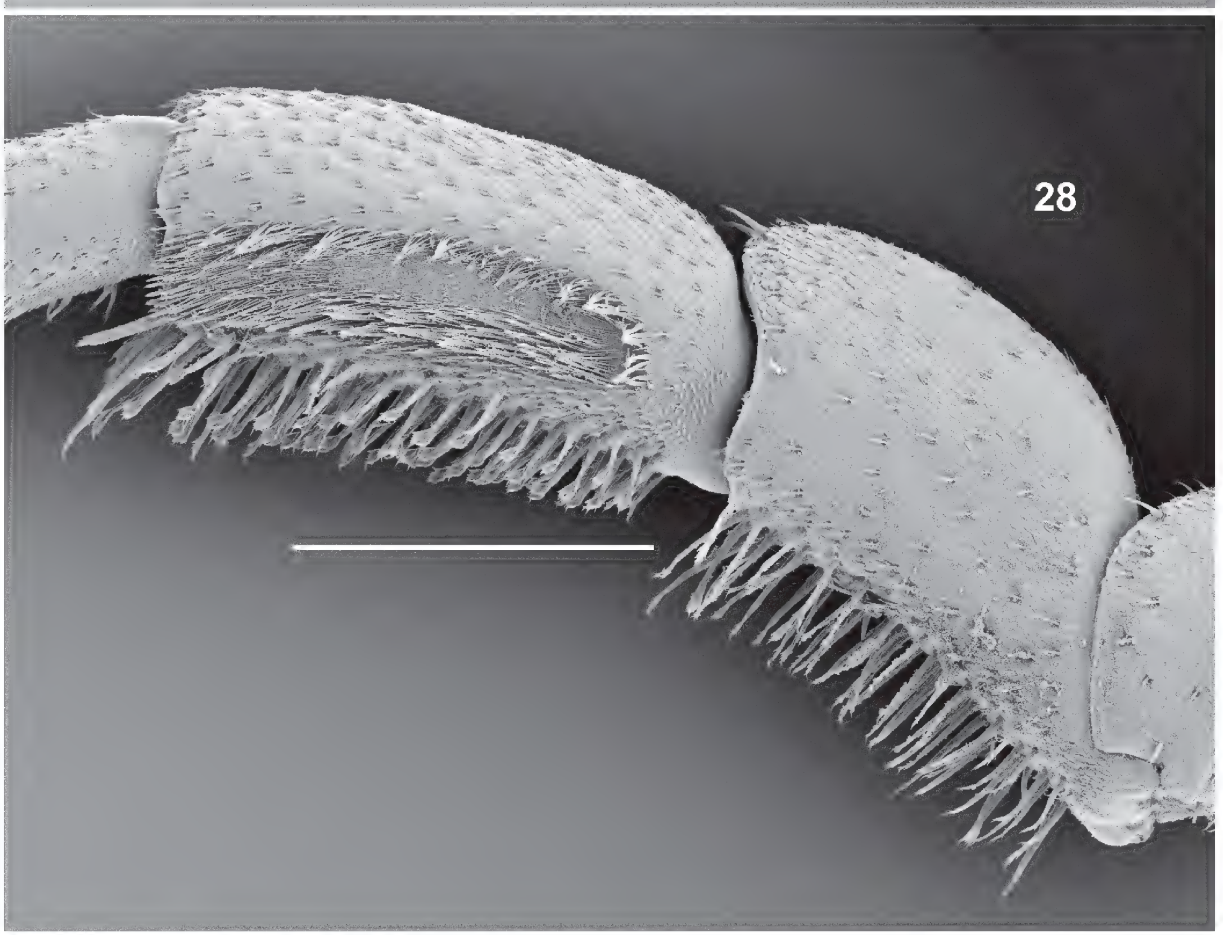
Cuticular structures: Tergites smooth or very slightly granulated (Fig. 25).

Frontal shield from behind surpassing frontal margin of head, upper margin rounded, no angles laterally, caudally with conspicuous groove (Fig. 25); antennal lobes trapezoidal (Fig. 26). Hind margin of pereion-epimeron 1 completely rounded (Fig. 31). Telson wider than long and with broadly rounded apex (Fig. 32). Antenna see Fig. 27, distal segment of the flagellum slightly longer than proximal one. Male pereiopod 1 with dense brush of spines on carpus and merus (Fig. 28); male ischium 7 ventrally slightly concave, frontally with large S-shaped distal hair-field, caudal side with ventral and proximal hair-fields, basipodite 7 with hairy setae along medial margin (Figs. 29–30). Male pleopod-exopodite 1 with short hind-lobe,

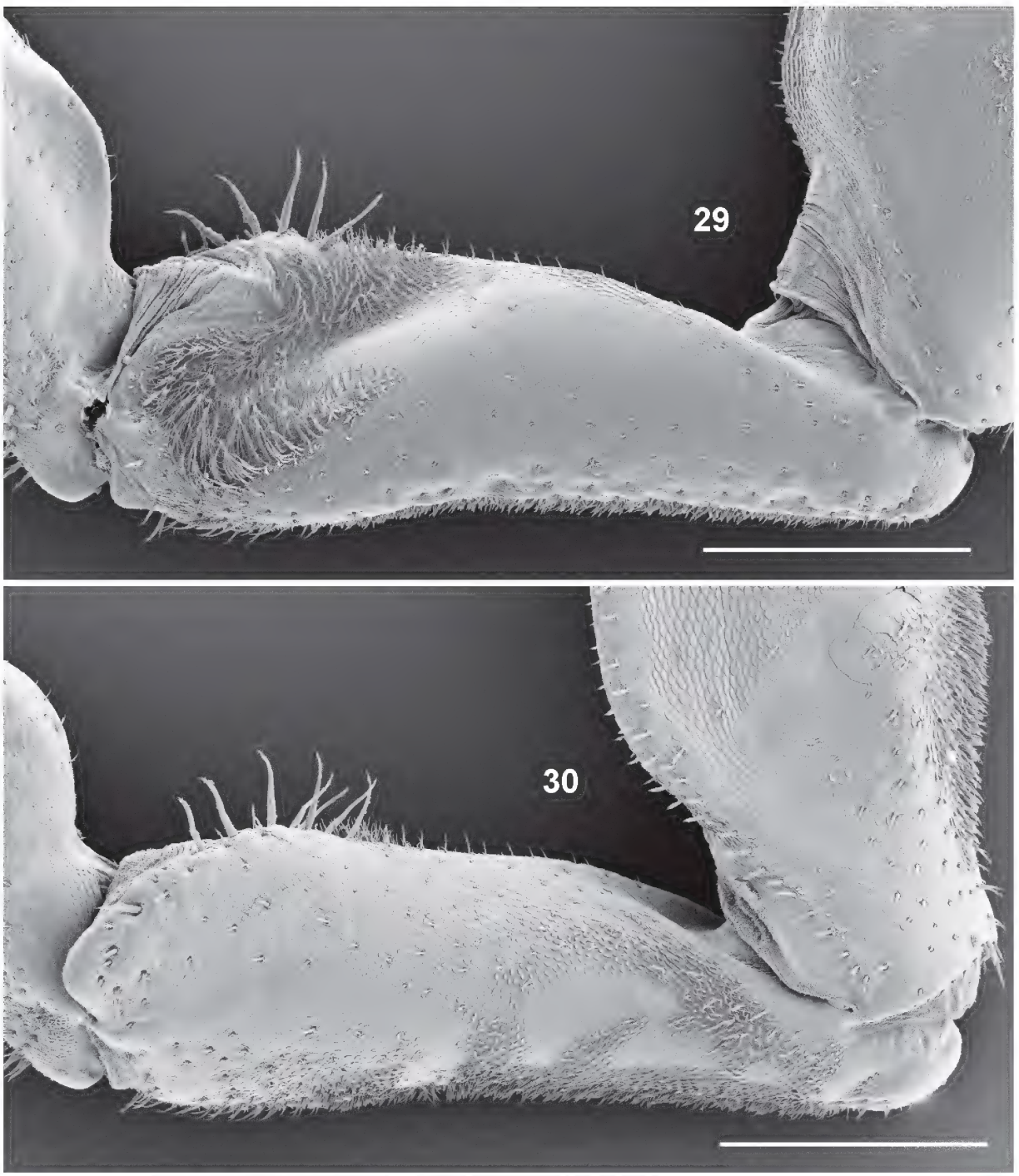


Figs. 25–26. *Armadillidium janinense* (northwestern Greece, Tímfi Mountain, SMNS 2751). – **25**. ♂, 15.2 × 7.0 mm, head, dorsal view. **26**. ♂, 13.3 × 6.2 mm, head, frontal view. – Scales: 1 mm.

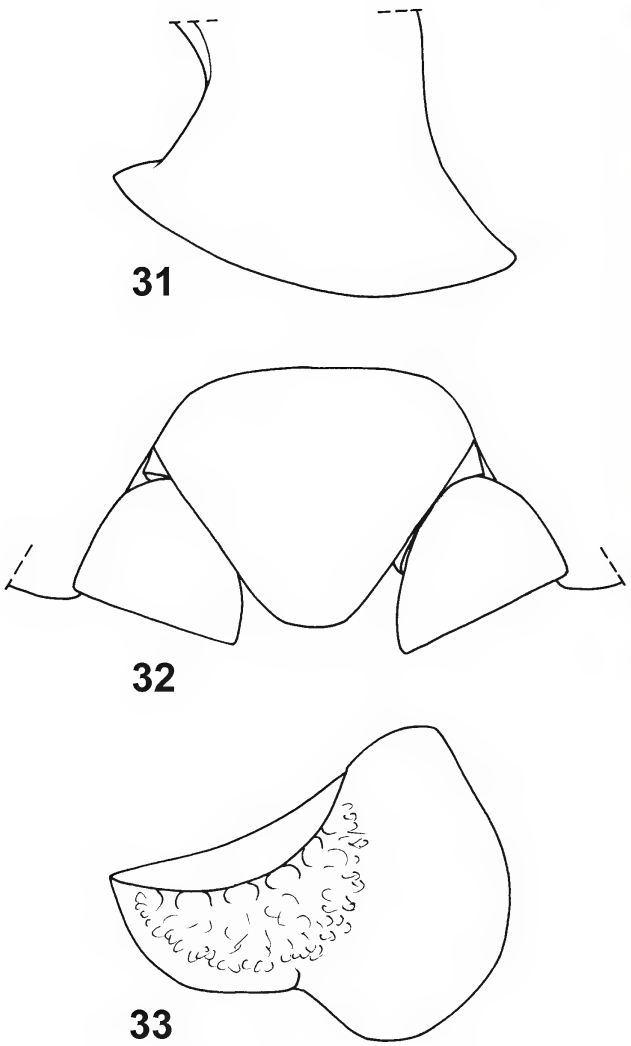




Figs. 27–28. *Armadillidium janinense* (northwestern Greece, Tímfi Mountain, SMNS 2751), ♂, 15.2 × 7.0 mm. – **27**. Antenna. **28**. Pereiopod 1, frontal view. – Scales: 0.5 mm.



Figs. 29–30. *Armadillidium janinense* (northwestern Greece, Tímfi Mountain, SMNS 2751), ♂, 15.2 × 7.0 mm. – **29**. Ischium 7, frontal view. **30**. Ischium 7, caudal view. – Scales: 0.5 mm.



Figs. 31–33. *Armadillidium janinense* (northwestern Greece, Tímfi Mountain, SMNS 2411), ♂, 13.0 × 5.8 mm. – **31**. Pereion-epimeron 1, lateral view. **32**. Telson and uropods in situ, dorsal view. **33**. Pleopod-exopodite 1, dorsal view.

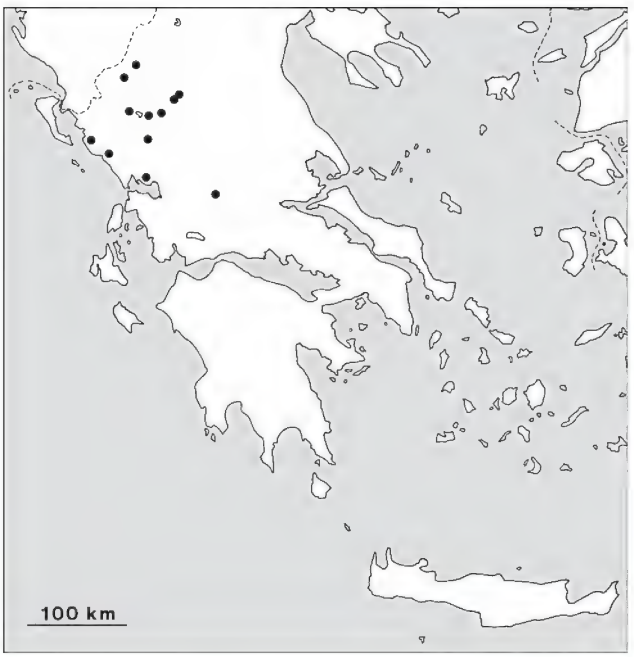


Fig. 34. Known records of *Armadillidium janinense*.

medial edge slightly concave (Fig. 33), endopodite 1 with apex straight. Uropod-exopodite terminally conspicuously straight-cut with sharp angles (Fig. 32).

Distribution

Known from the western Greek mainland (map Fig. 34), perhaps also occurring in southwestern ex-Yugoslavian Macedonia (see under Remarks).

Remarks

From the illustrations given by FRANKENBERGER (1941: 12) for *A. storkani* n. sp. from the Galičica Mountain in southwestern ex-Yugoslavian Macedonia this species seems to be identical with *A. janinense*. To be sure about this synonymy the type material of *A. storkani* should be re-investigated, the types are, however, not available.

All diagnostic characters of *A. janinense* show conspicuous similarities with the characters of *A. bensei* Schmalfuss, 2006 from the Peloponnese (compare SCHMALFUSS 2006a: 18ff.). The characters of the male pereiopod 7 are certainly common derived characters (synapomorphies) suggesting the two taxa to be sister species. Another species possessing the same derived hair-field structures is *A. granulatum* Brandt, 1833 (compare SCHMALFUSS 2006a: 29), so the three species possibly form a monophyletic group.

3.6 *Armadillidium jerrentrupi* **n. sp.**
(Figs. 35–46, map Fig. 47)

Material examined

Holotype: ♂, 18.5 × 8.5 mm, Greece, northern mainland, prefecture Xánthi, Néstos Gorge N of Toxótes, among boulders on the steep side of the river shore, high maquis vegetation, leg. SCHMALFUSS, 30.IV.1990 (SMNS T597).

Paratypes: 9 ♂♂, 8 ♀♀, 7 juv., same data as holotype (SMNS 2283). – 32 ex., same locality as holotype, leg. SCHAWALLER & SCHMALFUSS, 25.IV.1994 (SMNS 2435), leg. SCHMALFUSS, 18.X.2005 (SMNS 2864), 11.V.2006 (SMNS 1125). – 22 ex., Greece, northern mainland, prefecture Kavála, Lekáni Mountain, 2 km N of Polínero, mixed forest, leg. SCHMALFUSS, 6.V.1990 (SMNS 2271). – 21 ex., as before, 10 km N of Paleá Kavála, 600 m, maquis and *Castanea* forest, leg. SCHAWALLER & SCHMALFUSS, 20.IV.1994 (SMNS 2430).

Figs. 35–36. *Armadillidium jerrentrupi* n. sp., live animal, photographed by the author in 1990 in the Néstos Gorge near Toxótes (type locality). – **35**. Animal walking. **36**. Animal rolled-up.

Derivatio nominis

The species is dedicated to Hans Jerrentrup (Avramiliá, prefecture Kavála/Greece), who introduced me to the Néstos Gorge and to other fascinating biotopes in Greece.

Diagnostic characters

Maximum dimensions: 17.0 × 7.3 mm.

Coloration: Dark gray, the specimens from the Néstos Gorge with yellowish epimera and hind margins of tergites, the other samples uniformly gray.

Cuticular structures: Tergites smooth (Fig. 37).

Live animals see Figs. 35–36. Frontal shield from behind surpassing frontal margin of head, upper margin nearly straight, laterally with oblique rounded angles (Fig. 38); antennal lobes semicircular (Fig. 39). Hind margin of pereion-epimeron 1 with pronounced angle (Fig. 44). Telson longer than wide, with nearly straight sides and broadly truncate apex (Fig. 45). Antenna see Fig. 40, segments of the flagellum more or less the same length. Male carpus 1 with brush of short spines (Fig. 41); male ischium 7 ventrally straight, frontally with distal hair-field (Figs. 42–43). Male pleopod-exopodite 1 with short triangular hind-lobe (Fig. 46), endopodite 1 with apex straight. Uropod-exopodite with strongly rounded inner angle (Fig. 45).

Distribution

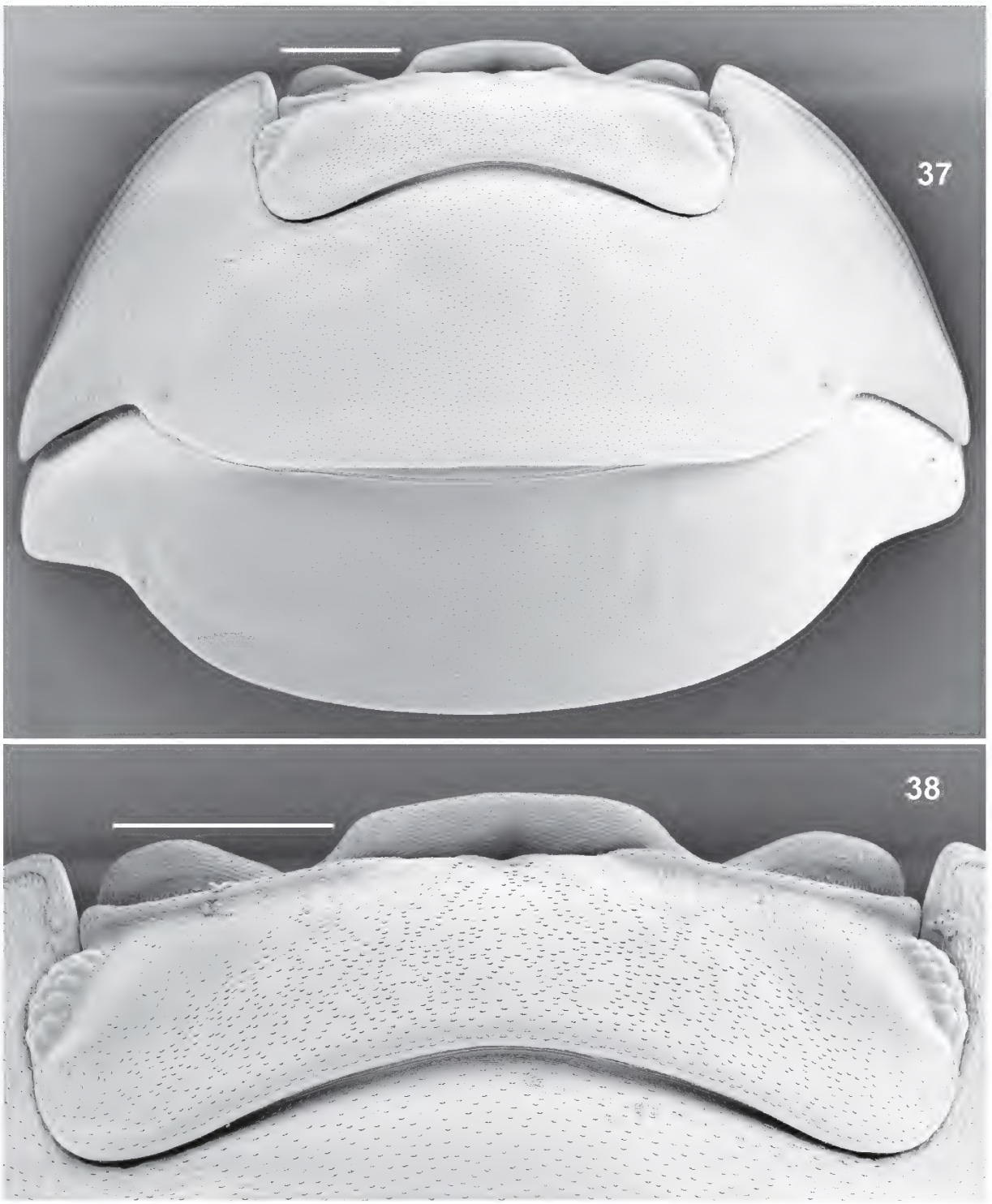
Northern Greek mainland, lower Néstos river system (map Fig. 47).

Remarks

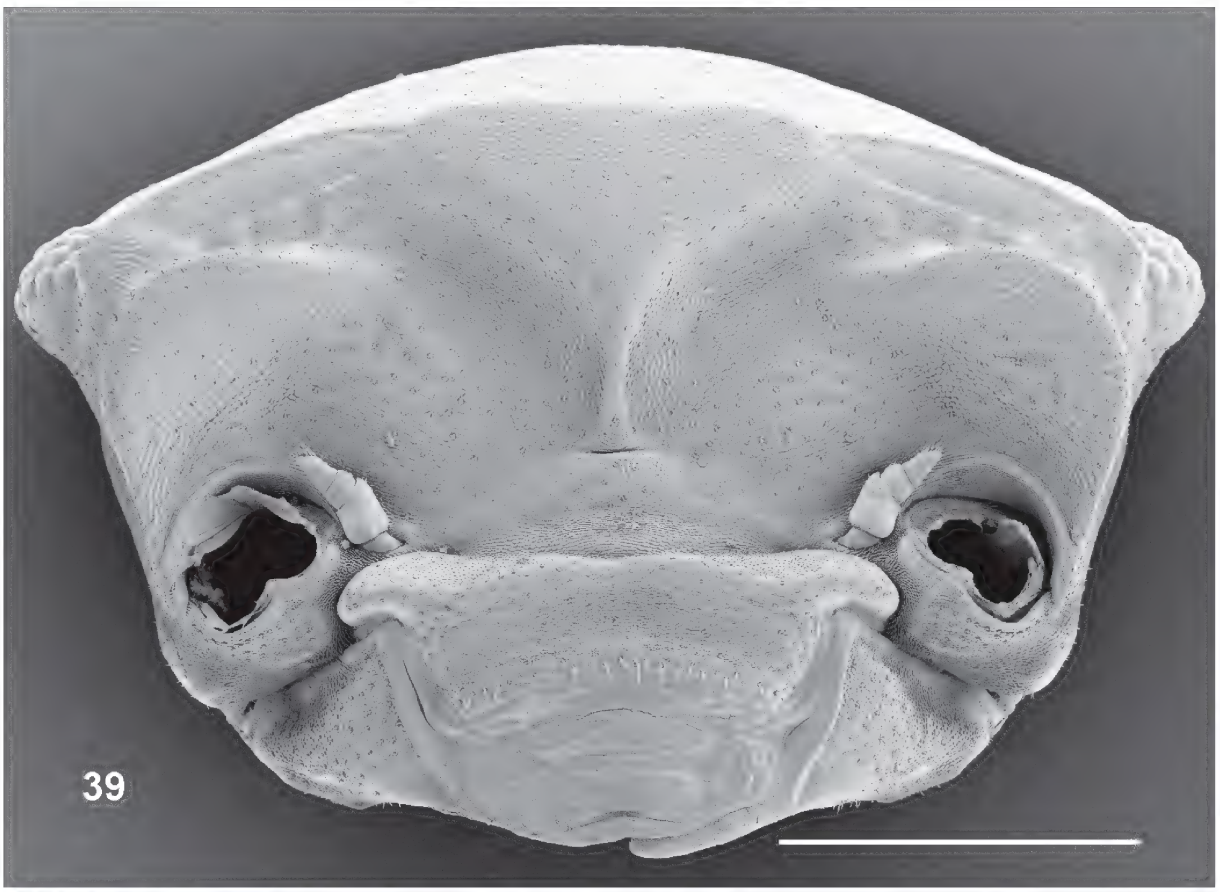
The new species seems to be a close relative of *A. fossuligerum*, considering the morphology of head, telson and male pleopods, it shows however clear differences indicating a separate species status. The coloration is different, the antenna is much more slender, the male ischium 7 is ventrally straight, not concave as in *A. fossuligerum*, and the uropod-exopodite is longer and has a strongly rounded inner angle. The allopatric distribution is further evidence for a sister group relationship.

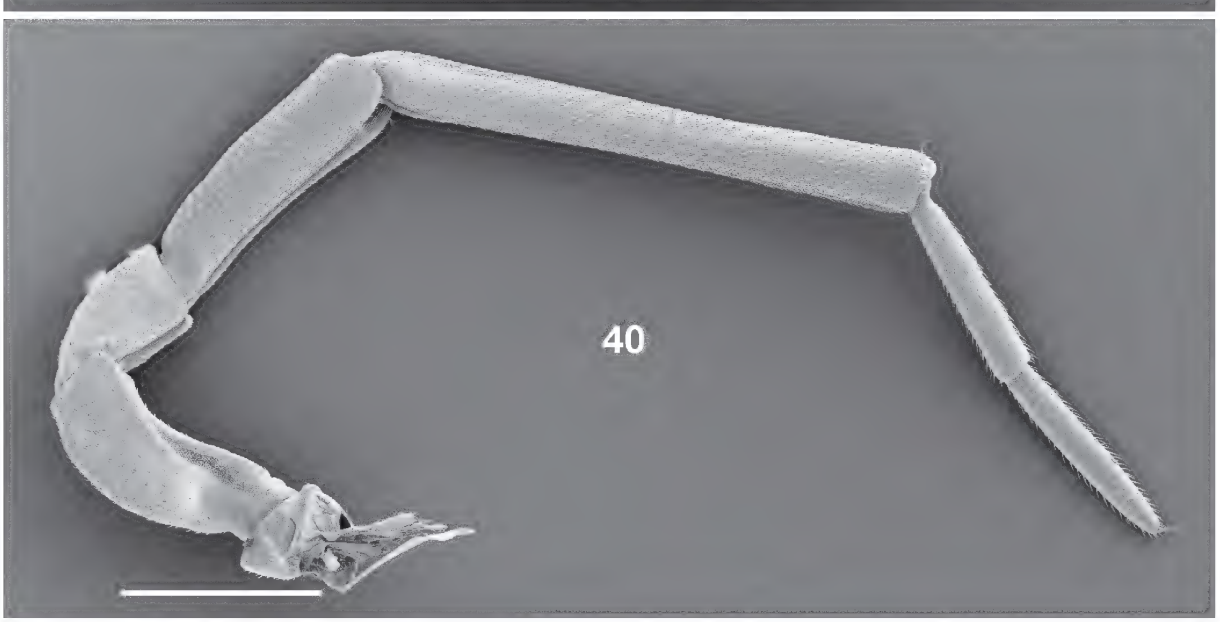
3.7 *Armadillidium marmoratum* Strouhal, 1929

This species was treated in the 23rd contribution of this series (Schmalfuss 2006a). It is known from the coasts of Greece (Ionian island Lefkáda, Peloponnese, Aegean islands, northern Aegean coast), western Turkey including Black Sea coast, Cyprus, Israel and Egypt. A map of the overall distribution is found in Schmalfuss (2000: 79, fig. 4), for safe Greek records see map fig. 153 in Schmalfuss (2006a).

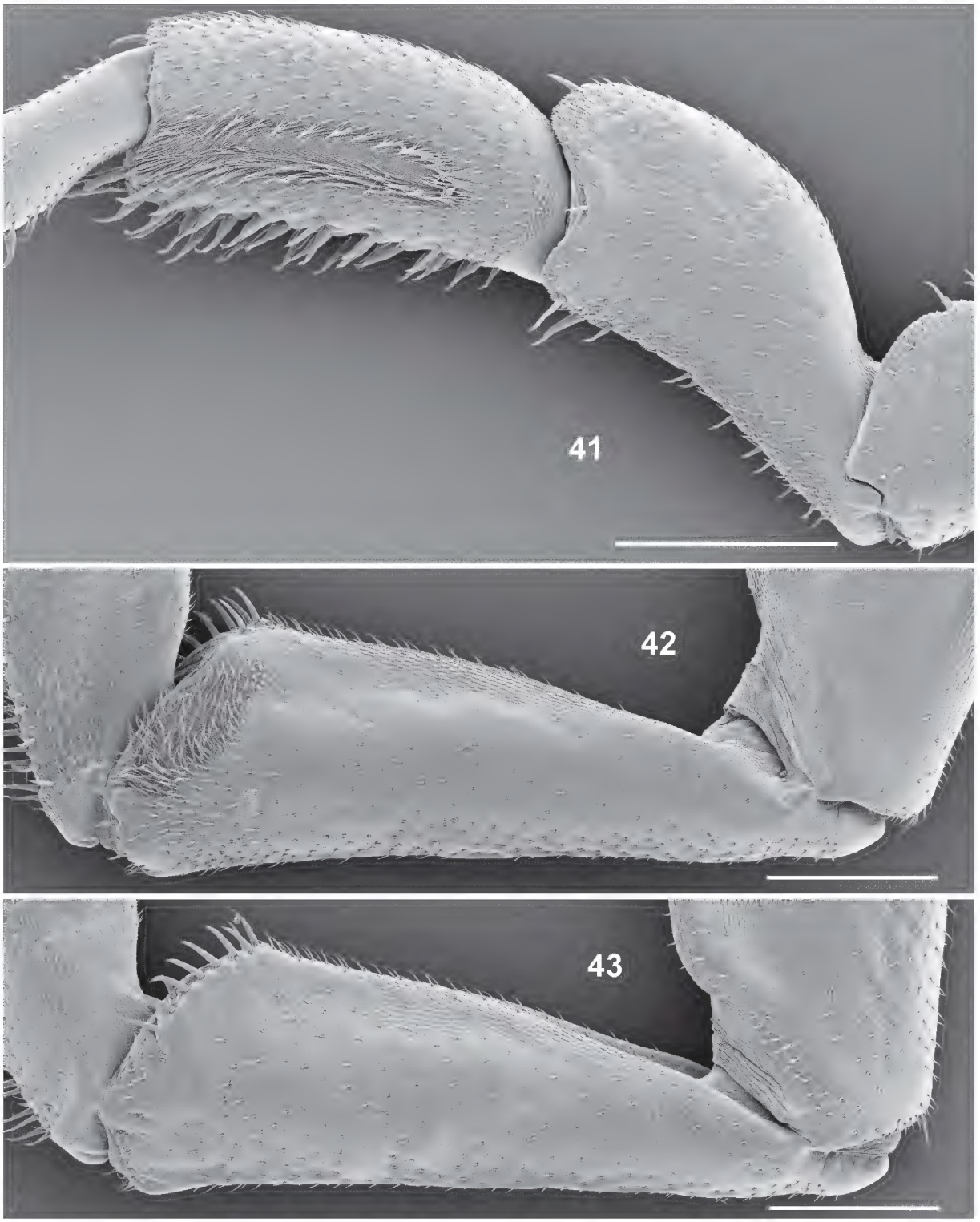


Figs. 37–38. *Armadillidium jerrentrupi* n. sp., ♂, 18.3 × 9.2 mm, paratype from type locality (Néstos Gorge, SMNS 2283). – **37**. Head and pereion-tergites 1 and 2, dorsal view. **38**. Head, dorsal view. – Scales: 1 mm.

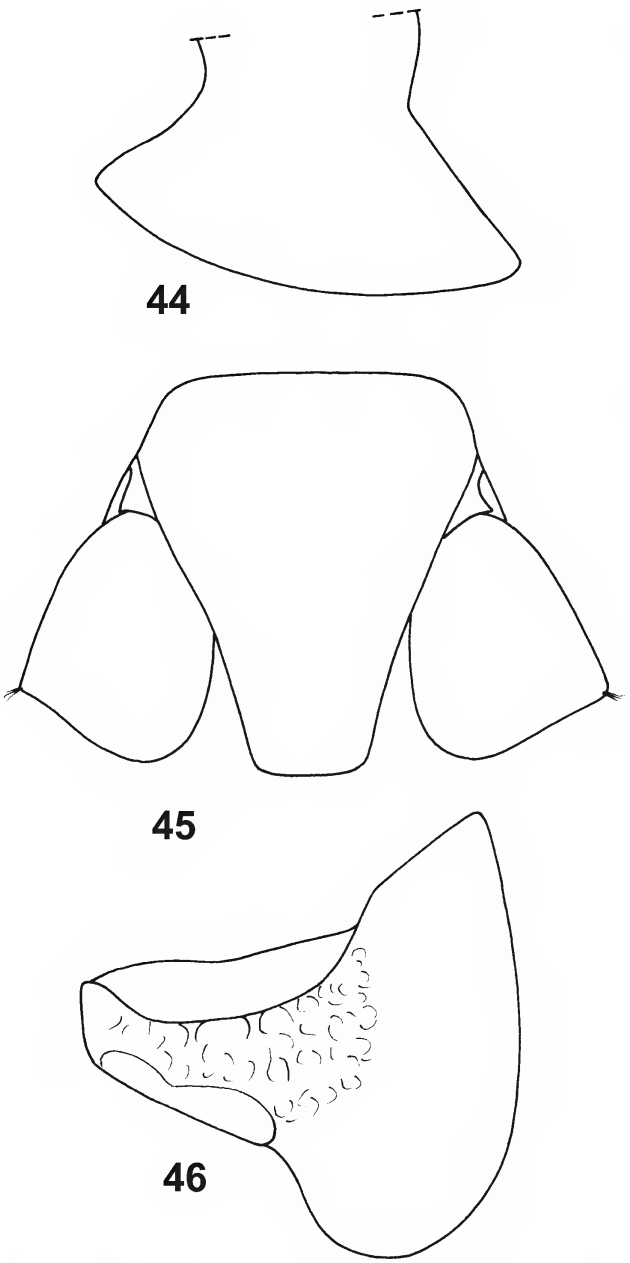




Figs. 39–40. *Armadillidium jerrentrupi* n. sp., paratypes from type locality (Néstos Gorge, SMNS 2283). – **39**. ♂, 16.0 × 7.5 mm, head, frontal view. **40**. ♂, 18.3 × 9.2 mm, antenna. – Scales: 1 mm.



Figs. 41–43. *Armadillidium jerrentrupi* n. sp., ♂, 18.3 × 9.2 mm, paratype from type locality (Néstos Gorge, SMNS 2283). – **41**. Pereiopod 1, frontal view. **42**. Ischium 7, frontal view. **43**. Ischium 7, caudal view. – Scales: 0.5 mm.



Figs. 44–46. *Armadillidium jerrentrupi* n. sp., ♂, 18.3 × 9.2 mm, paratype from type locality (Néstos Gorge, SMNS 2283). – **44**. Pereion-epimeron 1, lateral view. **45**. Telson and uropods in situ, dorsal view. **46**. Pleopod-exopodite 1, dorsal view.

3.8 *Armadillidium pangaionum* **n. sp.**
(Figs. 48–57, map Fig. 88)

Material examined

Holotype: ♂, 13.5 × 5.8 mm, Greece, northern mainland, prefecture Sérres, Pangéo Mountain, northern side, monastery Ikosifiníši, 500 m, mixed forest, leg. Schmalfuss, 4.V.1990 (SMNS T600).

Paratypes: 7 ex., same data as holotype (SMNS 2275). – 5 ex., same locality as holotype, leg. Pieper, 20.IV.1987 (SMNS 2165). – 1 ex., Pangéo Mountain, northern side, above Próti, 1100 m, *Fagus*, maquis, leg. Schmalfuss, 4.V.1990 (SMNS 2274), leg. Pieper, 11.V.1995 (SMNS 2529). – 12 ex., Pangéo Mountain, 1900 m, above timber line, alpine meadows, leg. Schmalfuss, 2.V.1990 (SMNS 2281). – 9 ex., Pangéo Mountain, eastern side, 1500–1600 m, *Fagus*, leg. Pieper, 19.IV.1987 (SMNS 2159), leg. Schmalfuss, 2.V.1990 (SMNS 2279). – 56 ex., Pangéo Mountain, eastern side, 1000–1300 m, leg. Manicastri, 4.V.1982 (SMNS 2698), leg. Osella, 20.VII.1983 (SMNS 2087), leg. Schmalfuss, 1.V.2002 (SMNS 2733). – 26 ex., Pangéo Mountain, eastern side, 650–900 m, *Fagus-Quercus* forest, leg. Schawaller & Schmalfuss, 30.IV.1994 (SMNS 2414), leg. Schmalfuss, 3.V.1990 (SMNS 2277, 2278). – 10 ex., prefecture Kavála, 5 km W of Eleftherúpoli, 400 m, *Quercus*, *Platanus*, leg. Schawaller & Schmalfuss, 29.IV.1994 (SMNS 2432). – 1 ex., prefecture Sérres, Néa Elvetía, leg. Pieper, 23.IV.1987 (SMNS 2161).

Derivatio nominis

The species is named after its main distribution area, the Pangéo Mountain in the eastern part of the province Macedonia.

Diagnostic characters

Maximum dimensions: 13.5 × 5.8 mm.

Coloration: Tergites dark gray with small light muscle-spots.

Cuticular structures: Tergites smooth with a very faint rugosity (Fig. 48).

Frontal shield from behind surpassing frontal margin of head, upper margin slightly rounded, with obtuse angles laterally, caudally with conspicuous groove (Fig. 49); antennal lobes semicircular (Fig. 50). Hind margin of pereion-epimeron 1 with pronounced obtuse angle (Fig. 44). Telson slightly longer than wide, with nearly straight sides and rounded apex (Fig. 45). Antenna see Fig. 40, distal segment of the flagellum slightly longer than proximal one. Male carpus 1 with brush of short spines (Fig. 52); male ischium 7 ventrally concave, frontally with distal and ventral hair-fields (Figs. 53–54). Male pleopod-exopodite 1 with hind-lobe elongated to a narrow pointed apex (Fig. 57), endopodite 1 with apex straight.

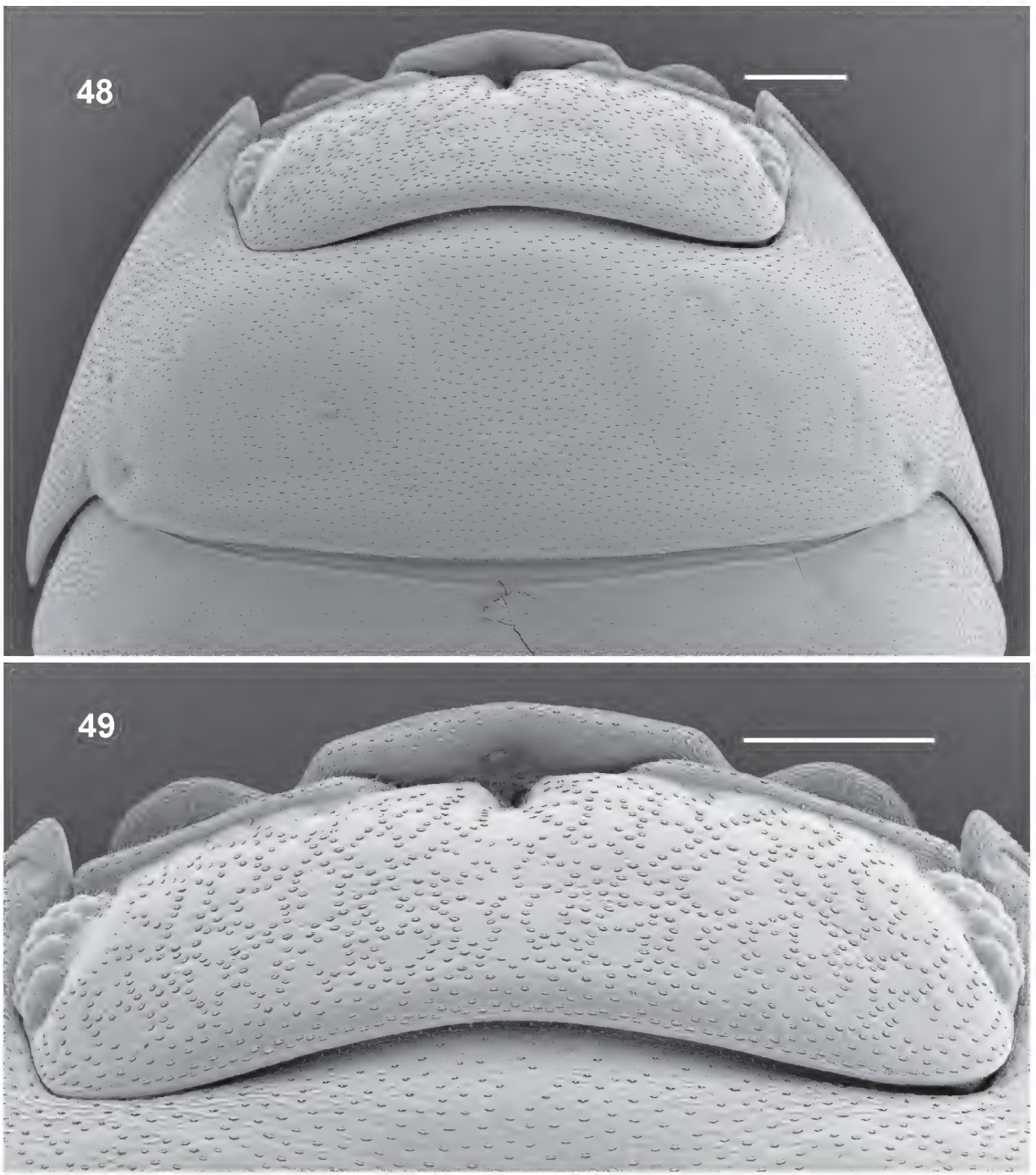
Distribution

Northern Greece, seems to be restricted to the region of the Pangéo Mountain (map Fig. 88).

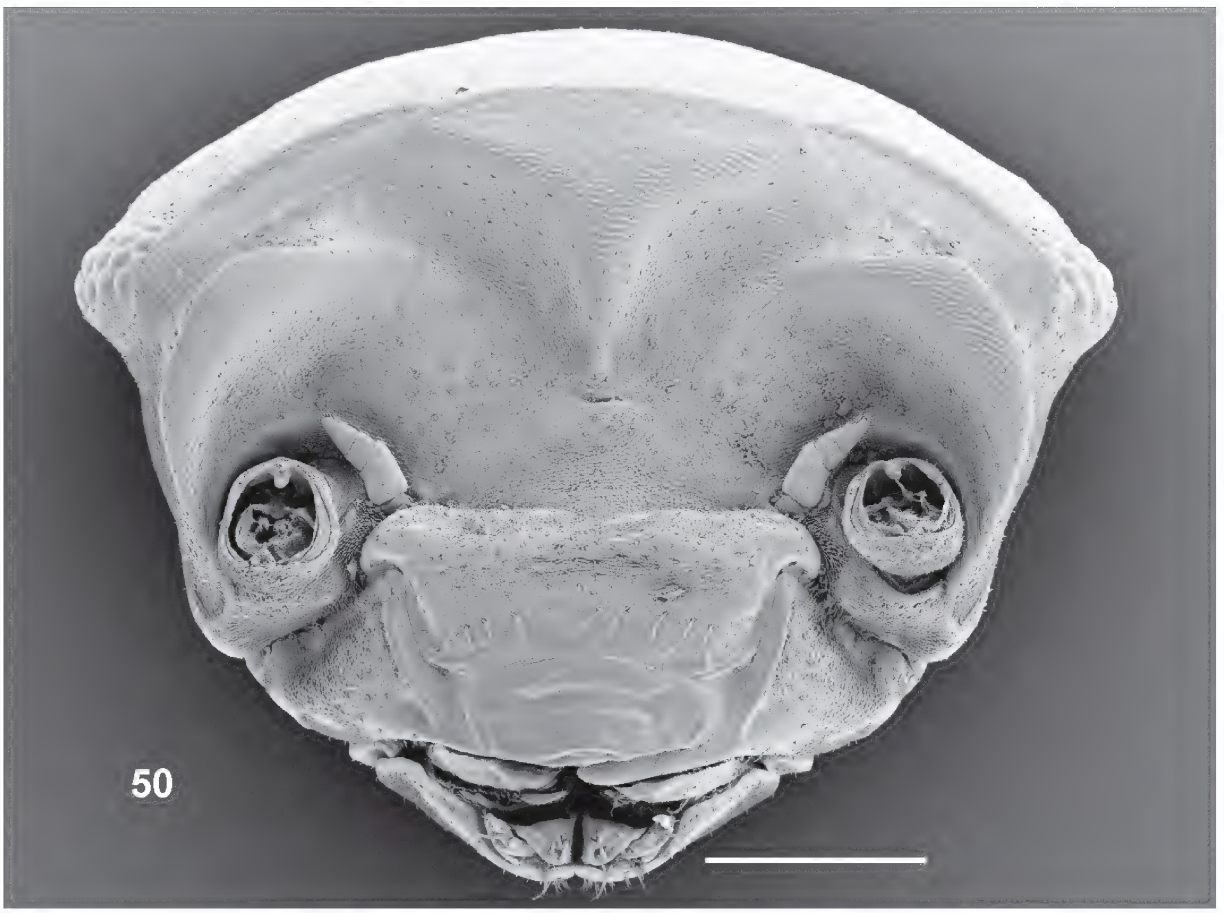
Remarks

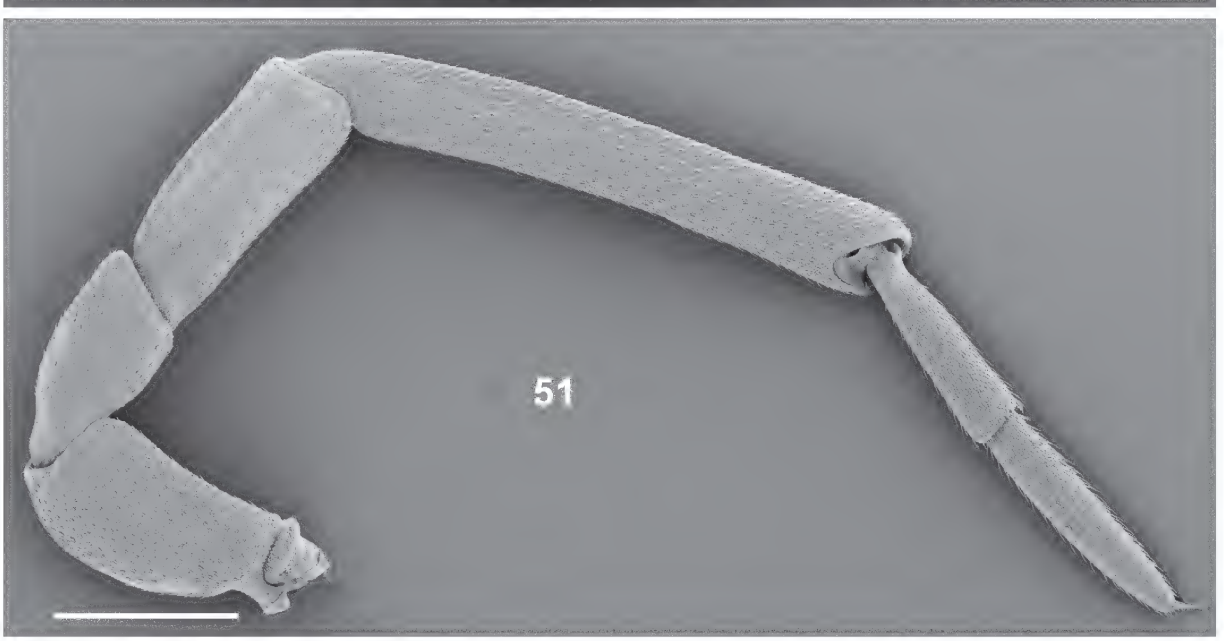
The species seems to be another member of the *insulanum*-group, which includes the species *insulanum*, *atticum* and *pelionense* (see Schmalfuss 2006b: 18, 32). The elongated hind-lobe of the male pleopod-exopodite 1 and a number of other differences (pereion-epimeron 1, telson, male ischium 7) indicate a separation on the species level.

Fig. 47. Known records of *Armadillidium jerrentrupi* n. sp. (●) and *A. pieperi* n. sp. (■).

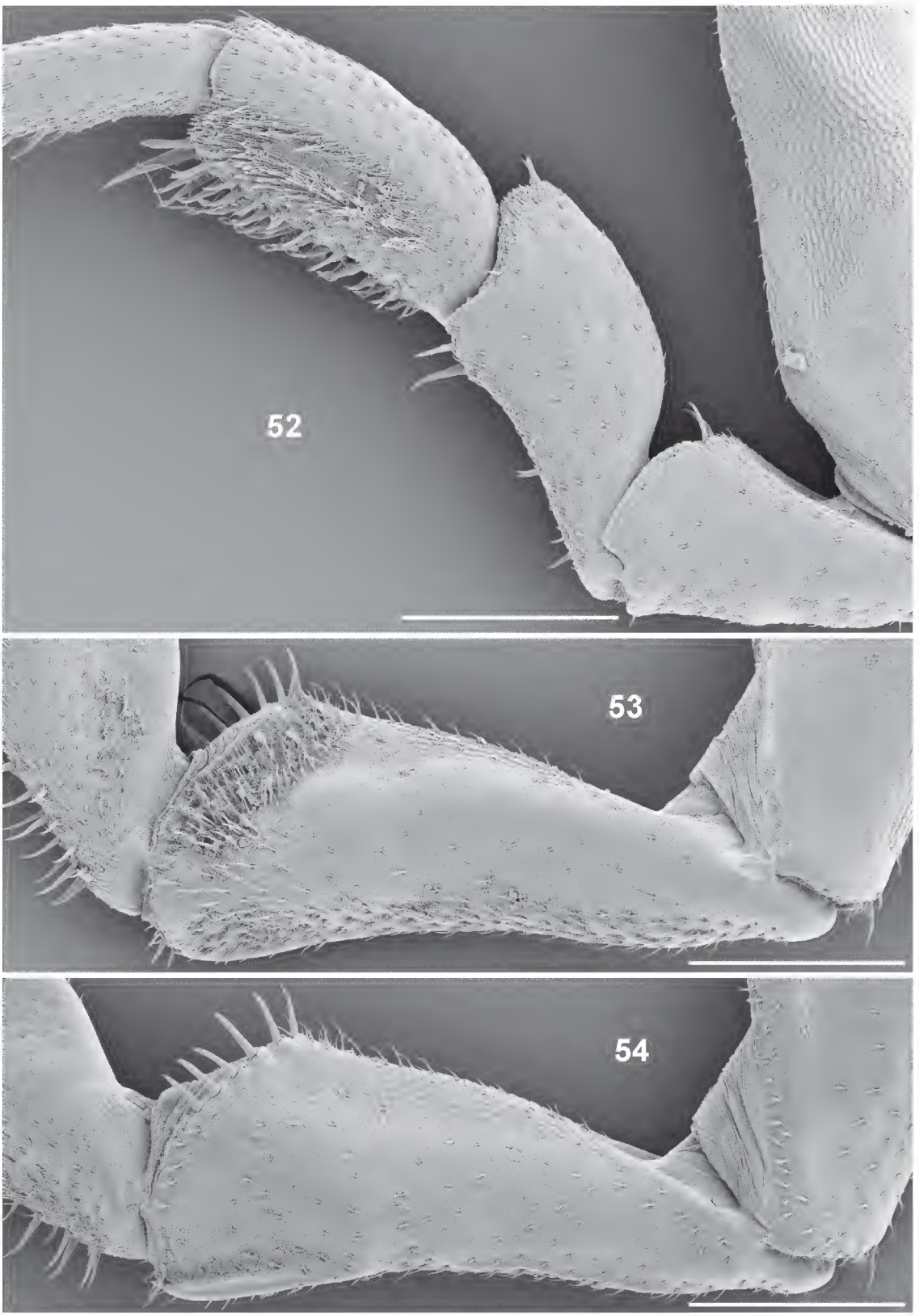


Figs. 48–49. *Armadillidium pangaionum* n. sp., ♂, 12.0 × 4.7 mm, paratype from Pangéo Mountain (SMNS 2414). – **48**. Head and pereion-tergite 1, dorsal view. **49**. Head, dorsal view. – Scales: 0.5 mm.

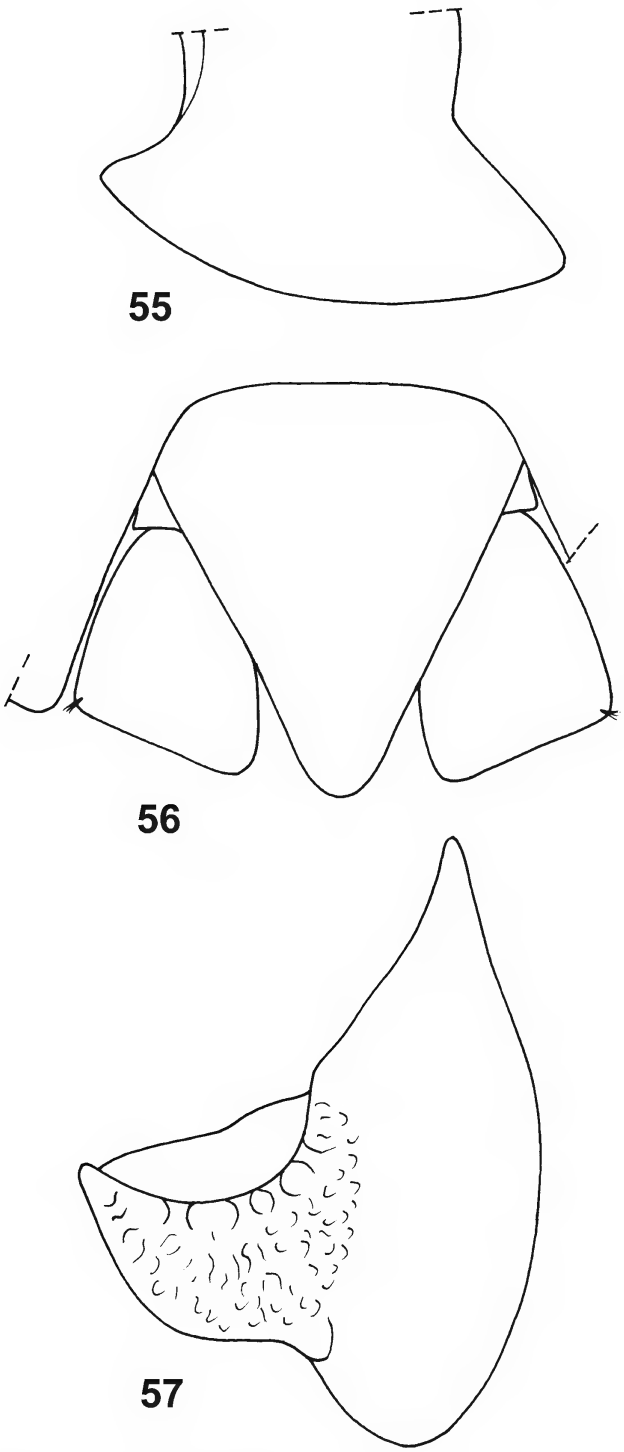




Figs. 50–51. *Armadillidium pangaionum* n. sp., paratypes from Pangéo Mountain (SMNS 2414). – **50**. ♂, 11.2 × 4.4 mm, head, frontal view. **51**. ♂, 12.0 × 4.7 mm, antenna. – Scales: 0.5 mm.



Figs. 52–54. *Armadillidium pangaionum* n. sp., ♂, 12.0 × 4.7 mm, paratype from Pangéo Mountain (SMNS 2414). – **52**. Pereiopod 1, frontal view. **53**. Ischium 7, frontal view. **54**. Ischium 7, caudal view. – Scales: 0.4 mm.



Figs. 55–57. *Armadillidium pangaionum* n. sp., ♂, 13.5 × 5.8 mm, holotype (SMNS T600). – **55**. Pereion-epimeron 1, lateral view. **56**. Telson and uropods in situ, dorsal view. **57**. Pleopod-exopodite 1, dorsal view.

3.9 *Armadillidium petralonense* **n. sp.**
(Figs. 58–67, map Fig. 68)

Material examined

Holotype: ♂, 15.0 × 7.2 mm, northern Greece, prefecture Khalkidikí, Petrálona, leg. Martens, 15.III.1963 (SMNS T601).

Paratypes: 2 ex., same data as holotype (SMNS 1500). – 7 ex., northern Greece, prefecture Thessaloníki, Thessaloníki, "Arsakli", leg. Kühnelt, III.1960 (SMNS 1685). – 7 ex., prefecture Khalkidikí, Galátista, leg. Pieper, 28.IX.1995 (SMNS 2534).

Derivatio nominis

The species' name refers to the locus typicus Petrálona (northern Greece, prefecture Khalkidikí).

Diagnostic characters

Maximum dimensions: 15 × 7 mm.

Coloration: Tergites gray with small yellowish muscle-spots, epimera yellowish gray.

Cuticular structures: Tergites smooth with a very faint rugosity (Fig. 58).

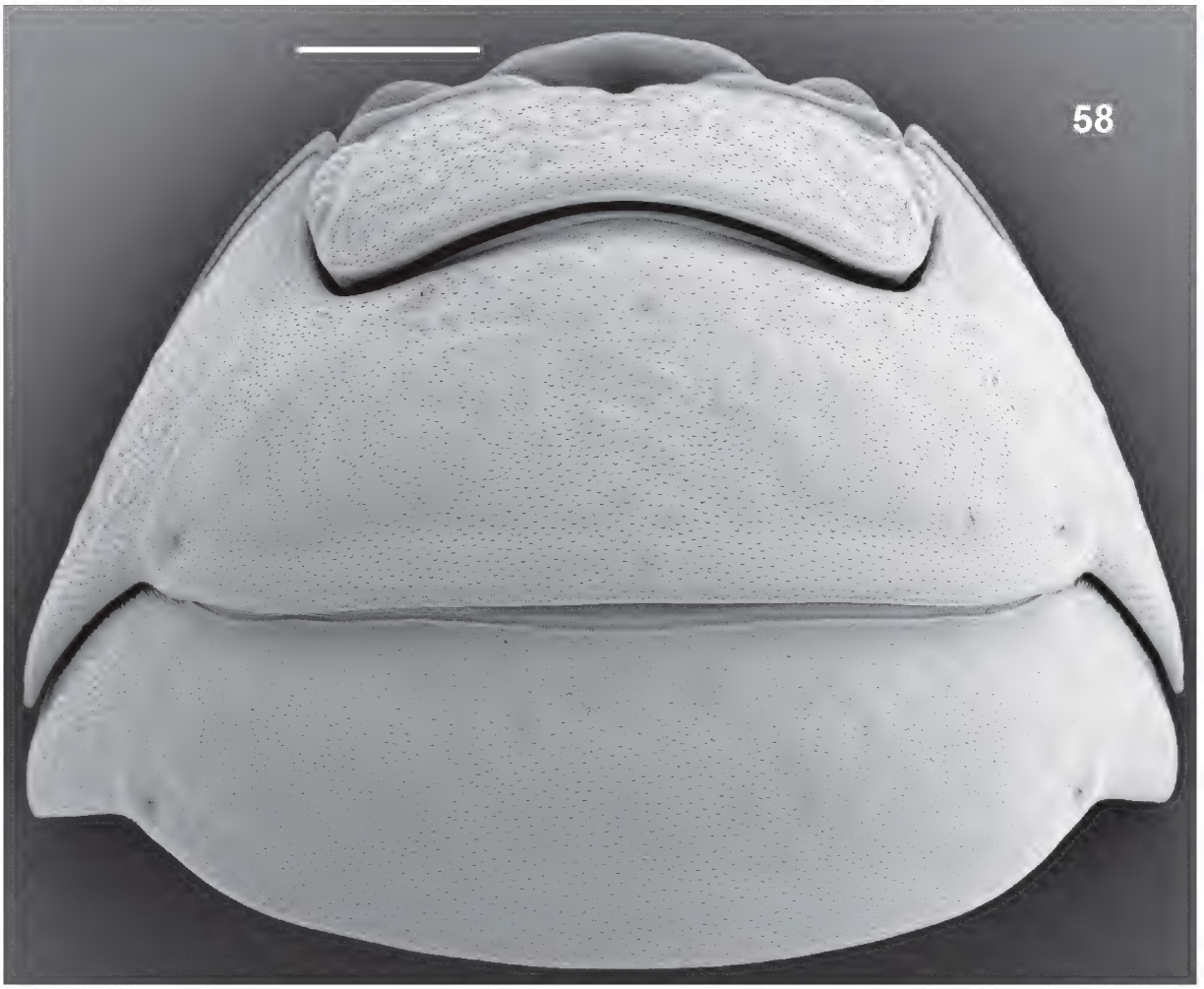
Frontal shield from behind surpassing frontal margin of head, upper margin completely rounded, no angles laterally, caudally with conspicuous groove (Fig. 59); antennal lobes semicircular (Fig. 60). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 65). Telson slightly longer than wide, with nearly straight sides and broadly rounded apex (Fig. 66). Antenna see Fig. 61, distal segment of the flagellum slightly longer than proximal one. Male carpus 1 with brush of short spines (Fig. 62); male ischium 7 ventrally straight, frontally with distal hair-field (Figs. 63–64). Male pleopod-exopodite 1 with triangular hind-lobe (Fig. 67), endopodite 1 with apex straight.

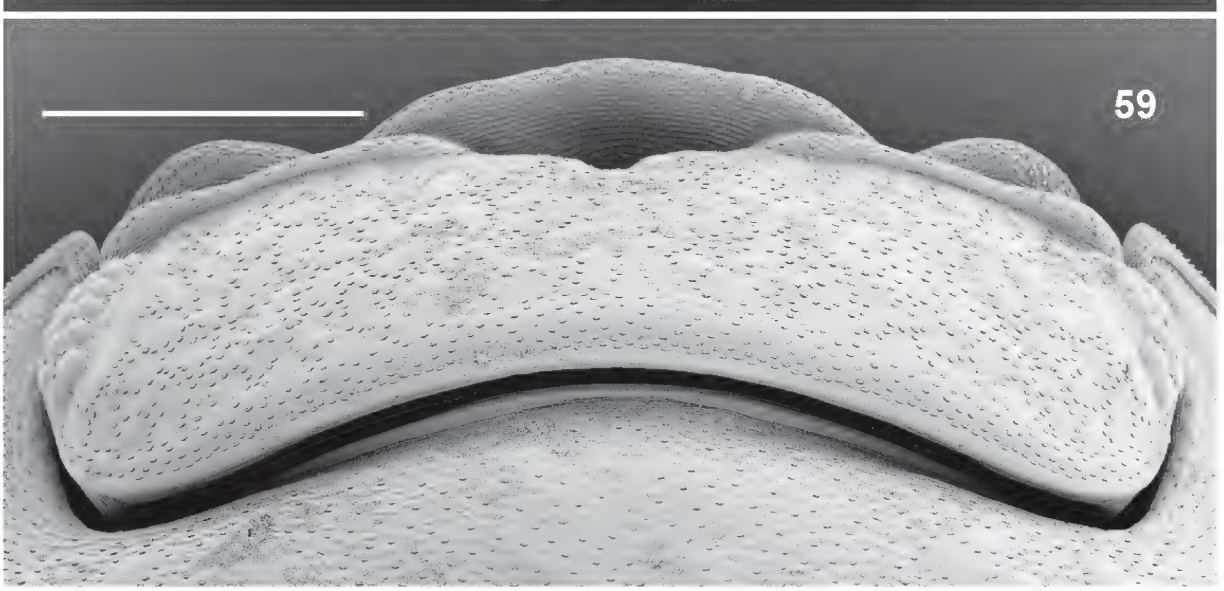
Distribution

Northern Greece, Khalkidikí and region east of Thessaloníki (map Fig. 68).

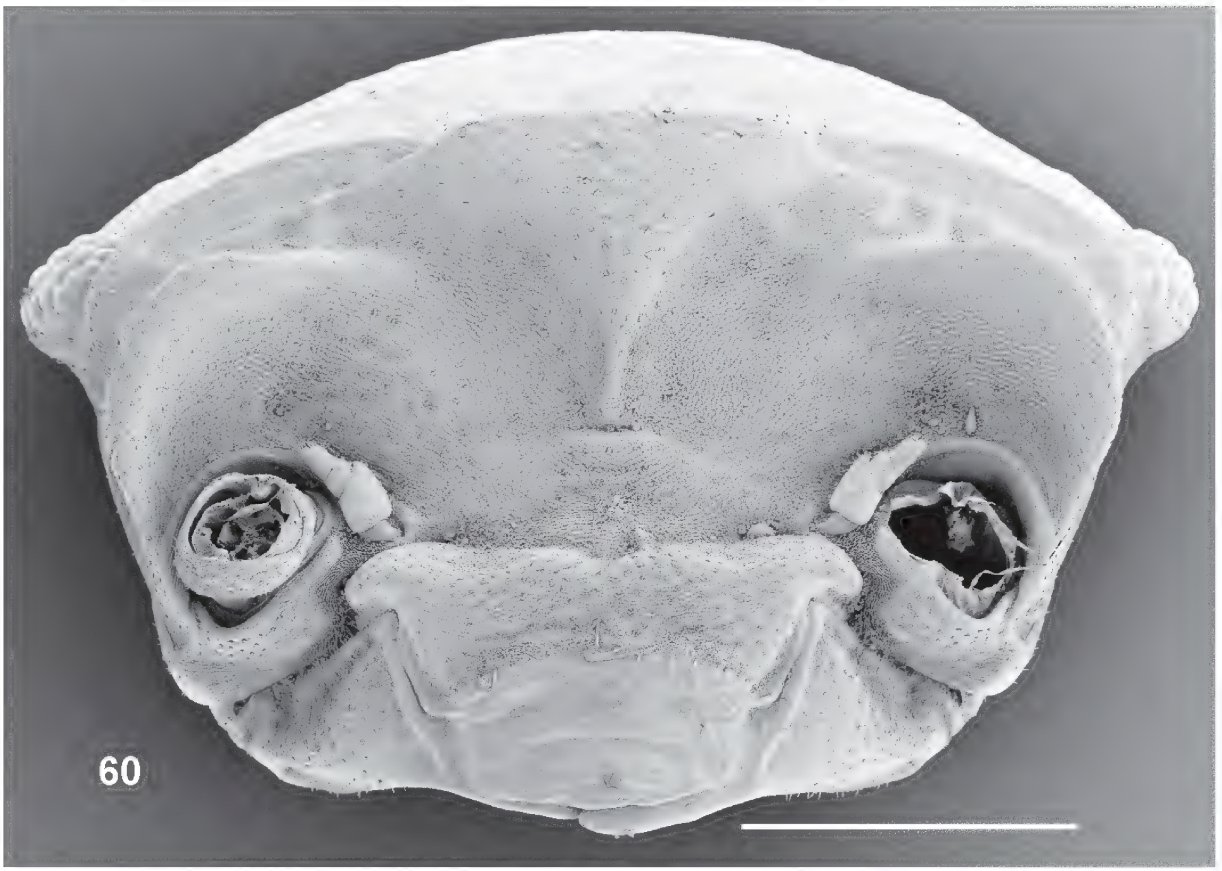
Remarks

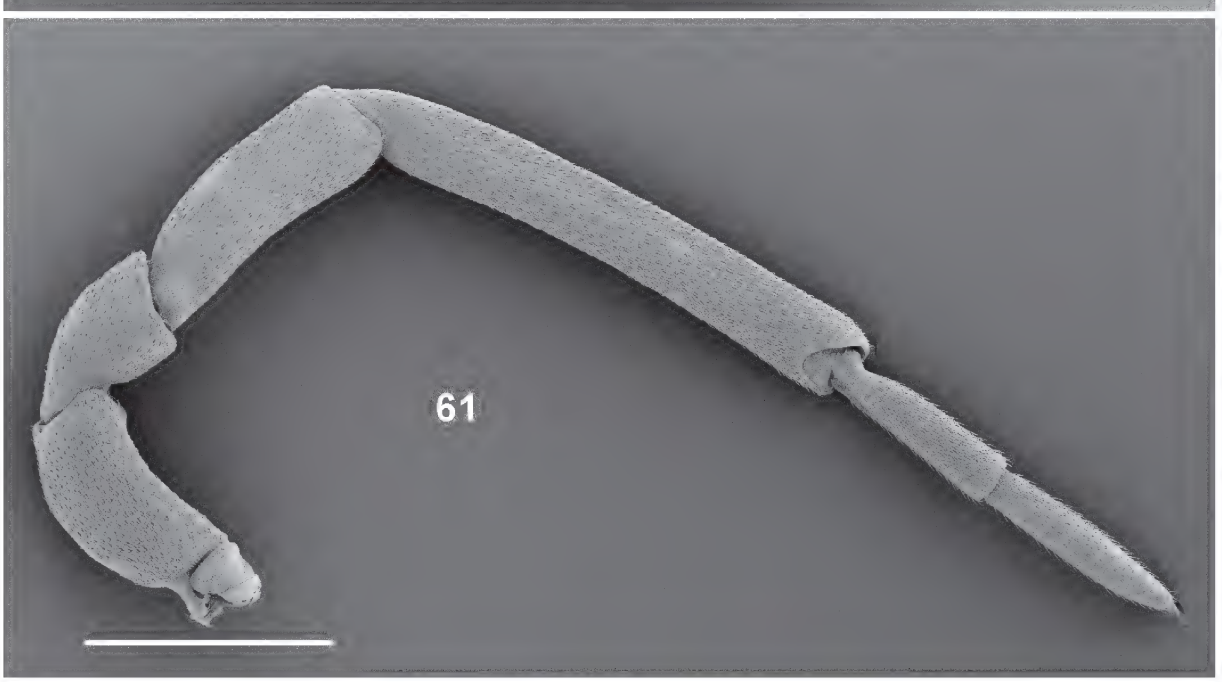
The species is very similar to *A. pieperi* n. sp., the differences in the shape of the male ischium 7 (ventrally strongly concave in *petralonense*, straight in *pieperi*) suggest, however, that we have to treat the two forms as separate species. The two species seem to belong to the *fossuligerum*-complex including *fossuligerum* and *jerrentrupi*, differing from the latter species of this group by the shape of the telson (pointed instead of truncate).



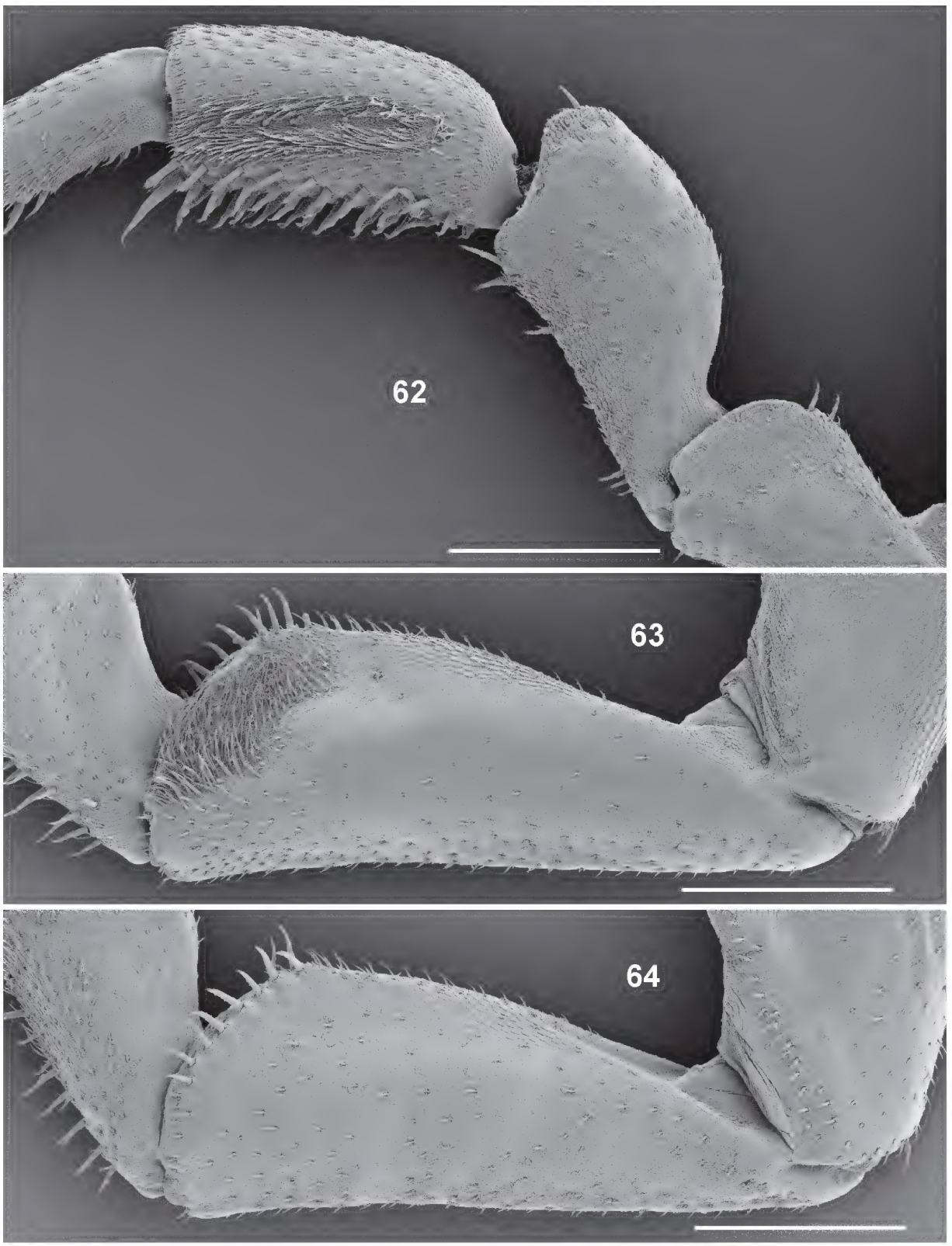


Figs. 58–59. *Armadillidium petralonense* n. sp., ♂, 15.2 × 7.0 mm, paratype from type locality (Petrálona, SMNS 1500). – **58**. Head and pereion-tergite 1, dorsal view. **59**. Head, dorsal view. – Scales: 1 mm.

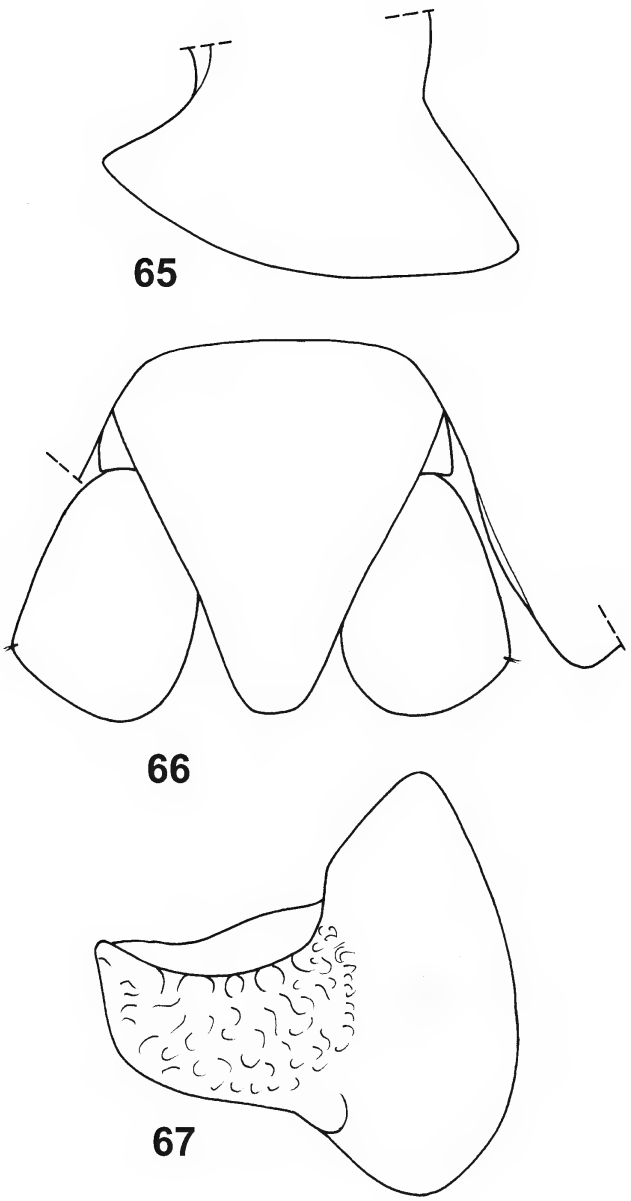




Figs. 60–61. *Armadillidium petralonense* n. sp., ♂, 15.2 × 7.0 mm, paratypes from type locality (Petrálona, SMNS 1500). – **60**. ♂, 14.0 × 6.7 mm, head, frontal view. **61**. ♂, 15.2 × 7.0 mm, antenna. – Scales: 1 mm.



Figs. 62–64. *Armadillidium petralonense* n. sp., ♂, 15.2 × 7.0 mm, paratype from type locality (Petrálona, SMNS 1500). – **62**. Pereiopod 1, frontal view. **63**. Ischium 7, frontal view. **64**. Ischium 7, caudal view. – Scales: 0.5 mm.



Figs. 65–67. *Armadillidium petralonense* n. sp., ♂, 15.3 × 7.2 mm, holotype (SMNS T601). – **65**. Pereion-epimeron 1, lateral view. **66**. Telson and uropods in situ, dorsal view. **67**. Pleopod-exopodite 1, dorsal view. – Scales: 0.5 mm.

3.10 *Armadillidium phalacronum* **n. sp.**
(Figs. 69–79, map Fig. 68)

Material examined

Holotype: ♂, 11 × 5 mm, Greece, northern mainland, prefecture Dráma, Falakró Mountain, western flank, 1300 m, *Fagus*, *Pinus*, leg. Schmalfuss, 30.IV.1990 (SMNS T598).

Paratypes: 28 ex., same data as holotype (SMNS 2426). – 2 ex., same locality as holotype, 1100 m, leg. Pieper, 21.IX.1995 (SMNS 2530). – 41 ex., same locality as holotype, 800 m, maquis, leg. Schmalfuss, 5.V.2002 (SMNS 2736). – 45 ex., Falakró Mountain, Khionótripa, 1700–1800 m, alpine meadows above timber line, leg. Schawaller & Schmalfuss, 19.IV.1994 (SMNS 2437), leg. Pieper, 21.IX.1995 (SMNS 2535). – 17 ex., Falakró Mountain, eastern flank, 8 km N of Livaderó, 650 m, deciduous forest, leg. Schmalfuss, 28.IV.1994 (SMNS 2434). – 1 ex., as before, 2 km S of Livaderó, leg. Pieper, 22.IV.1987 (SMNS 2157). – 28 ex., Falakró Mountain, southern flank, 400 m, maquis, leg. Schawaller & Schmalfuss, 28.IV.1994 (SMNS 2422). – 7 ex., prefecture Dráma, Rodópi Mountains, 5 km W of Elatiá, 1600 m, *Fagus-Pinus* forest, leg. Schmalfuss, 28.IV.1994 (SMNS 2436).

Derivatio nominis

The species' name refers to its distribution area, which is the Falakró Mountain and its immediate neighborhood to the north.

Diagnostic characters

Maximum dimensions: 12.5 × 5.5 mm.

Coloration: Brownish gray, sometimes light spots at bases of epimera.

Cuticular structures: Tergites nearly completely smooth (Fig. 69).

Frontal shield from behind surpassing frontal margin of head, upper margin nearly straight, obtuse angles laterally, caudally with conspicuous groove (Fig. 70); antennal lobes semicircular (Figs. 71–72). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 77). Telson wider than long, with straight sides and rounded apex (Fig. 78). Antenna see Fig. 73, distal segment of the flagellum somewhat longer than proximal one. Male carpus 1 with faintly developed brush of short spines (Fig. 74); male ischium 7 ventrally slightly concave, frontally with distal hair-field (Figs. 75–76). Male pleopod-exopodite 1 with triangular hind-lobe (Fig. 79), endopodite 1 with apex straight.

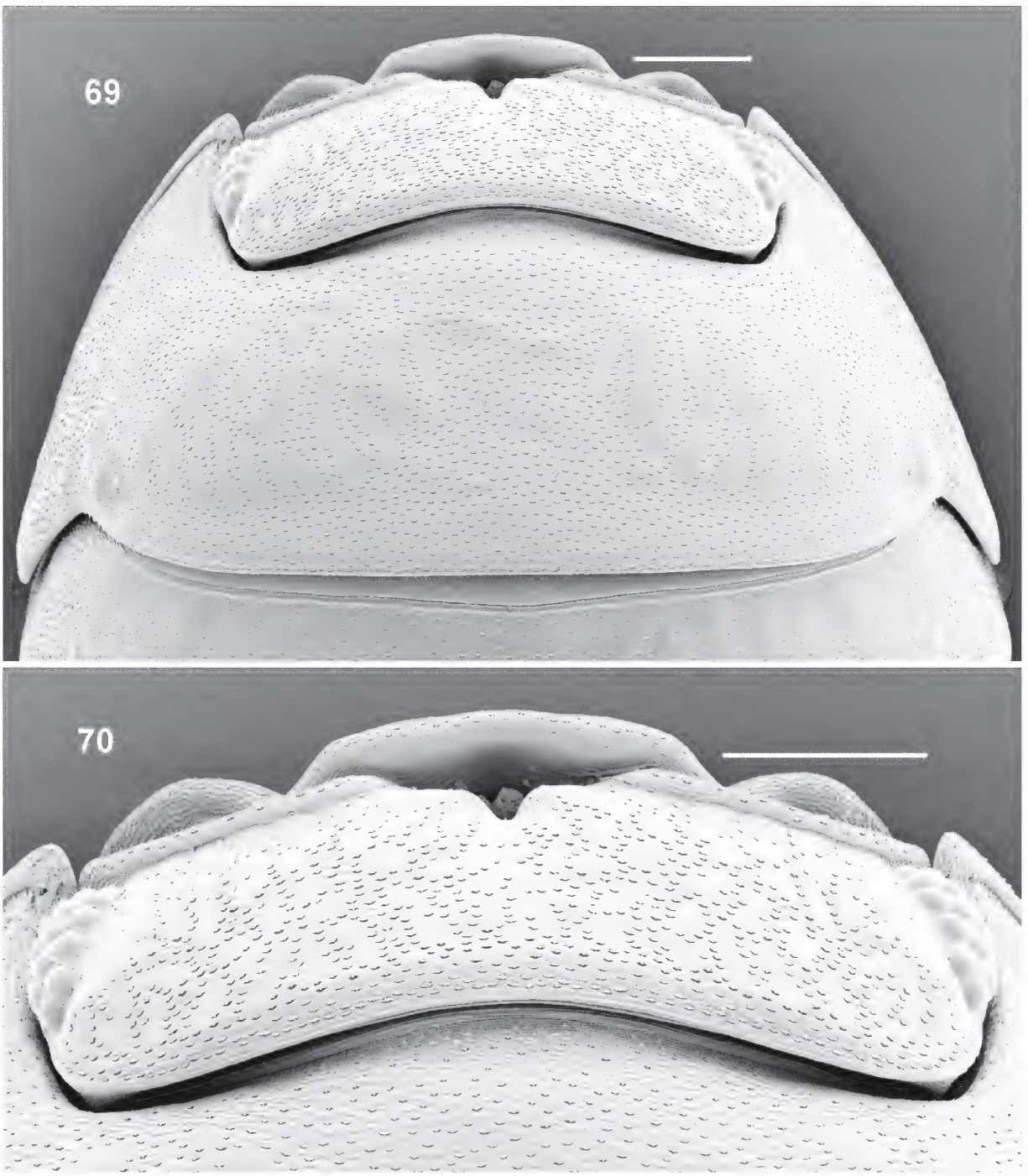
Distribution

Northern Greece, Falakró Mountain and southern slope of western Rodópi Mountains (map Fig. 66).

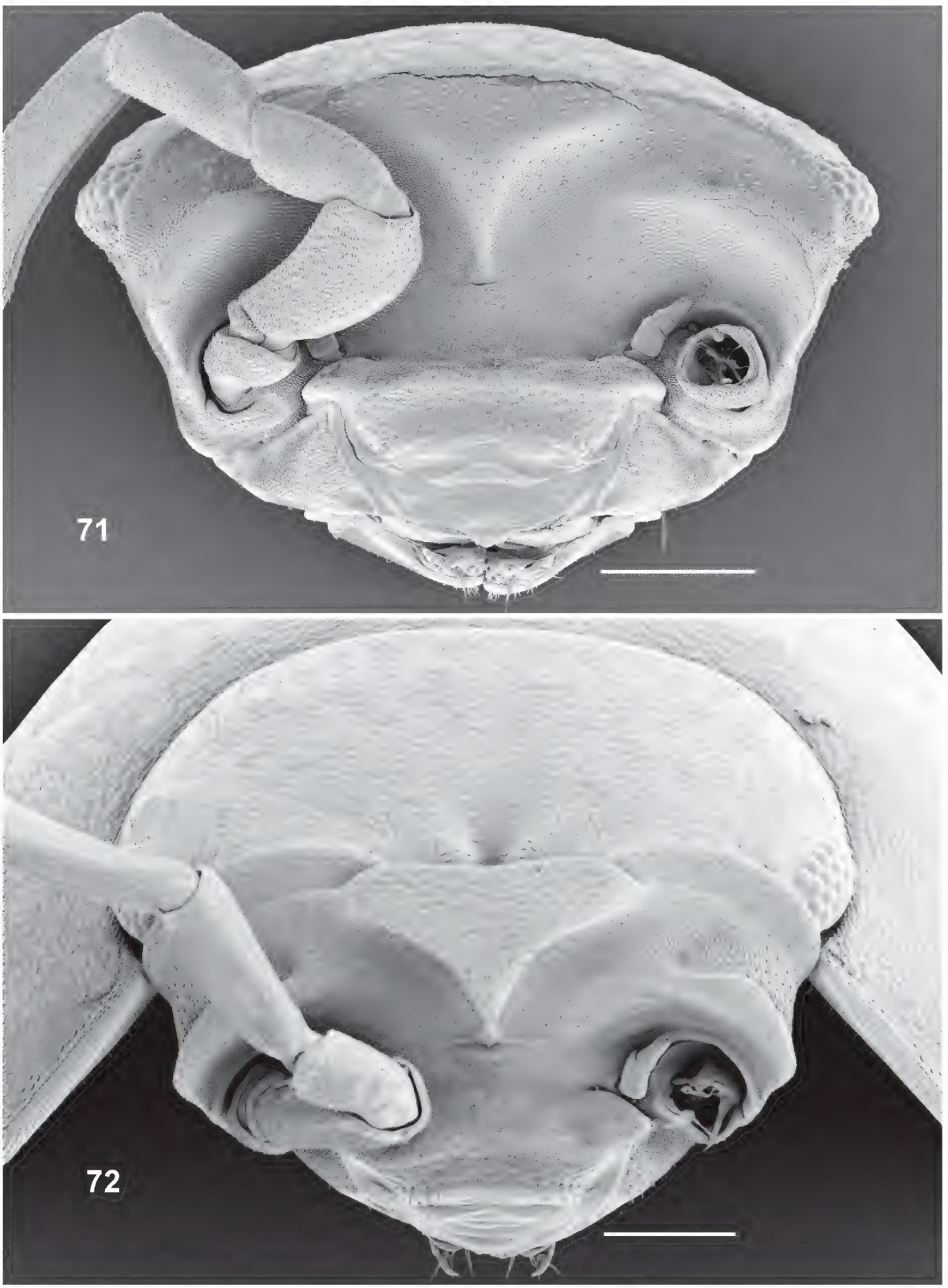
Remarks

The species is very close to *A. insulanum*. Because of slight morphological differences (*phalacronum*: rounded instead of straight upper margin of frontal triangle, rounded instead of trapezoidal antennal lobes, male pleopod-exopodite 1 with a conspicuously longer hind-lobe) I consider *A. phalacronum* a different taxon on the species level,

Fig. 68. Known records of *Armadillidium petralonense* n. sp. (●) and *A. phalacronum* n. sp. (■).



Figs. 69–70. *Armadillidium phalacronum* n. sp., ♂, 10.5 × 4.7 mm, paratype from type locality (Falakró Mountain, SMNS 2426). – **69**. Head and pereion-tergite 1, dorsal view. **70**. Head, dorsal view. – Scales: 0.5 mm.



Figs. 71–72. *Armadillidium phalacronum* n. sp., paratypes from type locality (Falakró Mountain, SMNS 2426). – **71**. ♀, 11.2 × 5.2 mm, head, frontal view. **72**. ♂, 13.0 × 5.5 mm, head, oblique frontal view. – Scales: 0.5 mm.

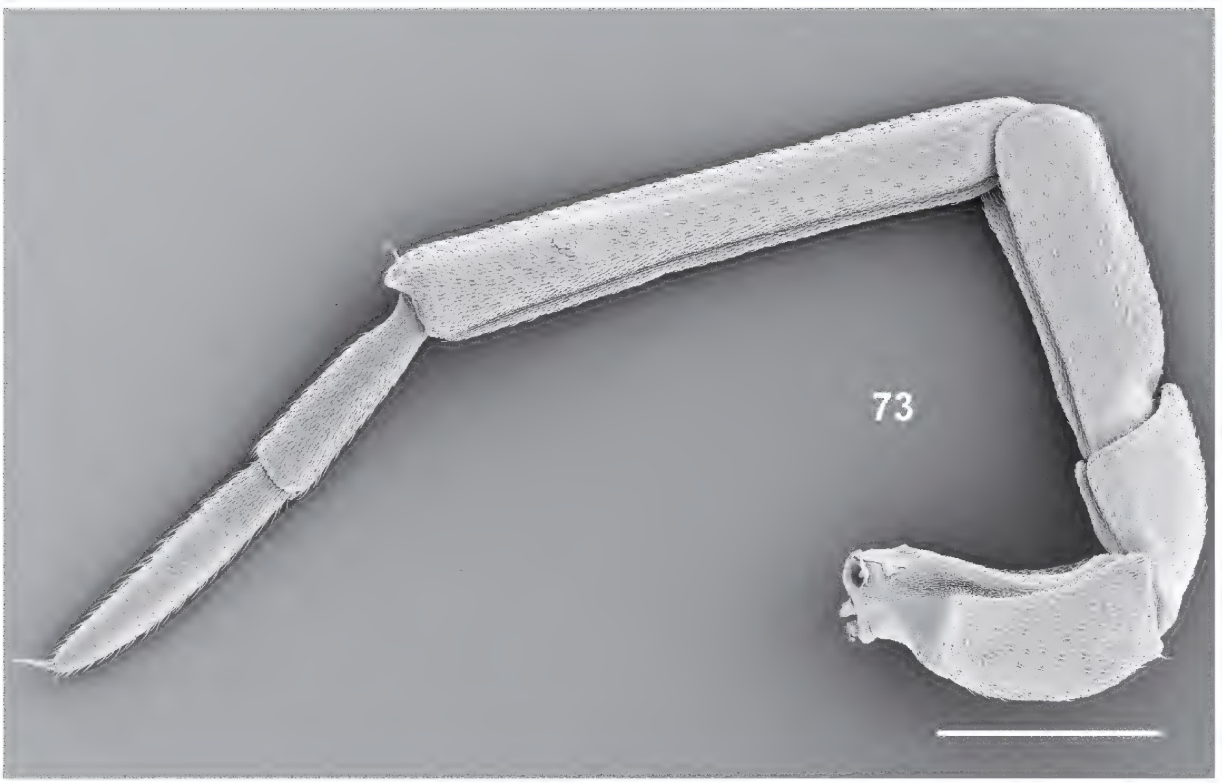
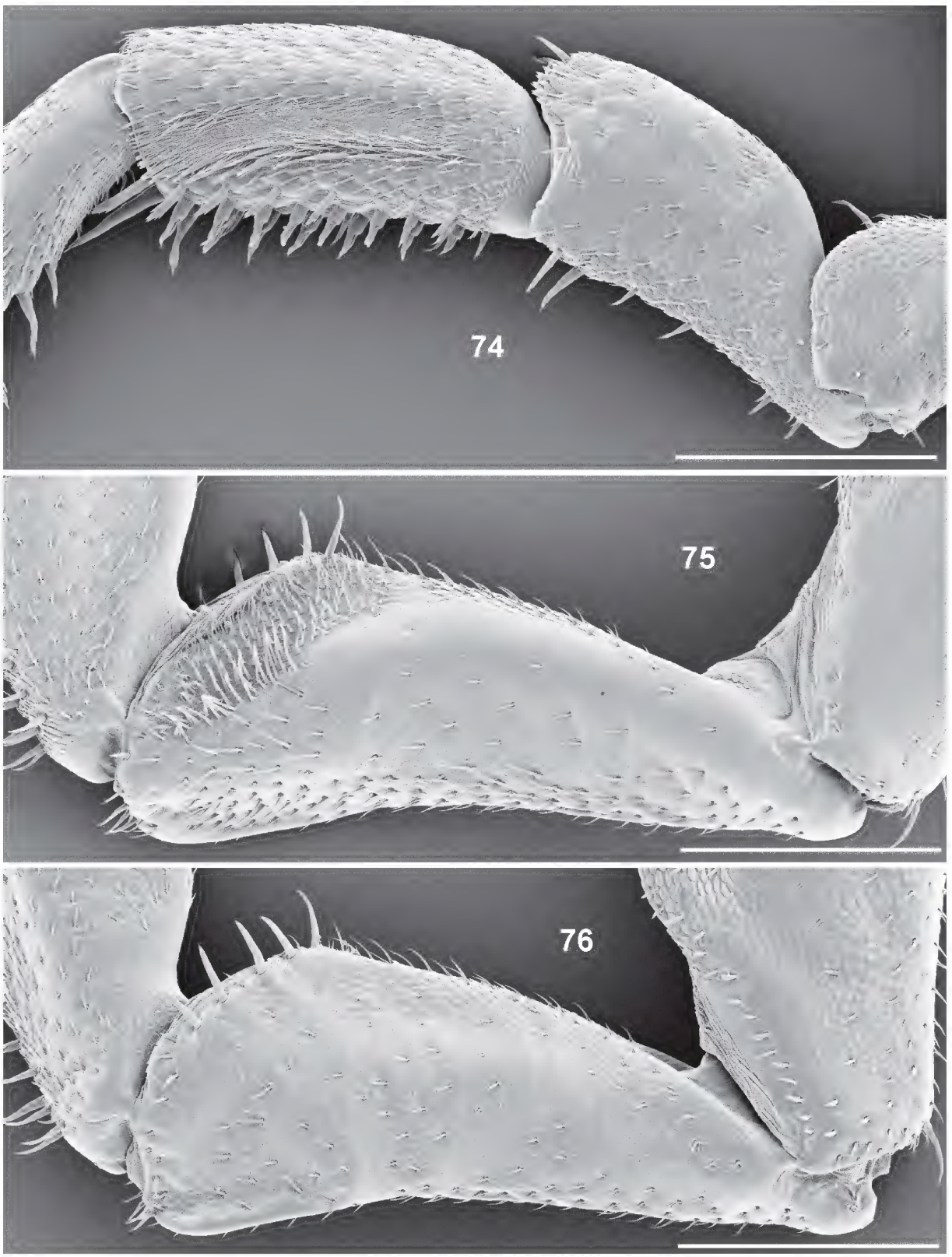
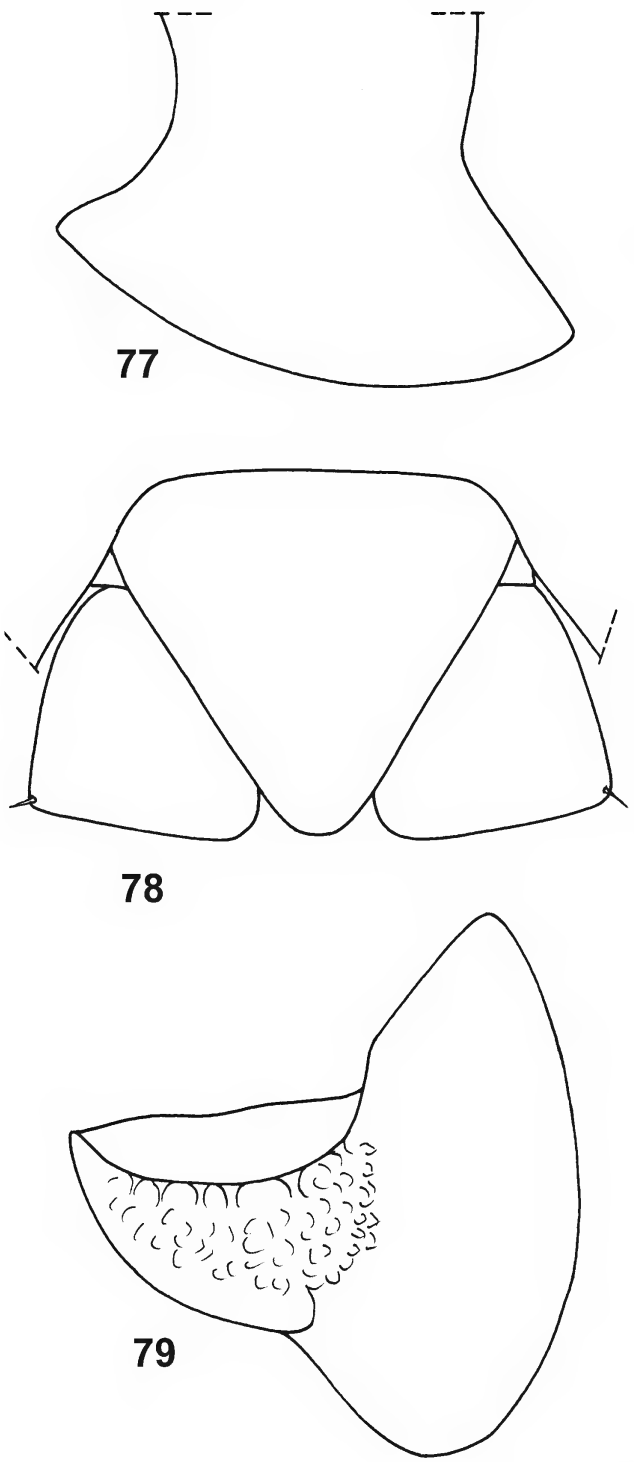


Fig. 73. *Armadillidium phalacronum* n. sp., ♂, 10.5 × 4.7 mm, paratype from type locality (Falakró Mountain, SMNS 2426), antenna. – Scale: 0.5 mm.



Figs. 74–76. *Armadillidium phalacronum* n. sp., ♂, 10.5 × 4.7 mm, paratype from type locality (Falakró Mountain, SMNS 2426). – **74**. Pereiopod 1, frontal view. **75**. Ischium 7, frontal view. **76**. Ischium 7, caudal view. – Scales: 0.4 mm.

further investigations including molecular data should clarify this questionable point.



Figs. 77–79. *Armadillidium phalacronum* n. sp., ♂, 10.5 × 4.7 mm, paratype from type locality (Falakró Mountain, SMNS 2426). – **77**. Pereion-epimeron 1, lateral view. **78**. Telson and uropods in situ, dorsal view. **79**. Pleopod-exopodite 1, dorsal view.

3.11 *Armadillidium pieperi* **n. sp.**
(Figs. 80–87, map Fig. 47)

Material examined

Holotype: ♂, 12.2 × 5.5 mm, Greece, northern mainland, prefecture Khalkidikí, peninsula Sithonía, 1 km S of Pórto Kufós, leg. Pieper, 26.IX.1995 (SMNS T603).

Paratypes: 2 ex., same data as holotype (SMNS 2531). – 3 ex., as before, peninsula Kassándra, 12 km W of Paliúri, leg. R. Grimm, 30.VII.1980 (SMNS 1900).

Derivatio nominis

The species is named after Dr. Harald Pieper (Kiel/Germany), whose extensive isopod collections have considerably enlarged our knowledge on the distribution of these animals in Greece.

Diagnostic characters

Maximum dimensions: 17.0 × 6.7 mm.

Coloration: Tergites grayish brown, epimera lighter.

Cuticular structures: Tergites faintly tuberculated (Fig. 80).

Frontal shield from behind surpassing frontal margin of head, upper margin completely rounded, no angles laterally, caudally with conspicuous groove (Fig. 80); antennal lobes trapezoidal (Fig. 81). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 85). Telson as wide as long, with nearly straight sides and rounded apex (Fig. 86). Antenna see Fig. 82, distal segment of the flagellum slightly longer than proximal one. Male carpus 1 with very few short spines (Fig. 83); male ischium 7 ventrally concave, frontally with distal hair-field (Fig. 84). Male pleopod-exopodite 1 with triangular hind-lobe (Fig. 87), endopodite 1 with apex straight.

Distribution

Northern Greece, Khalkidikí, peninsulas Kassándra and Sithonía (map Fig. 47).

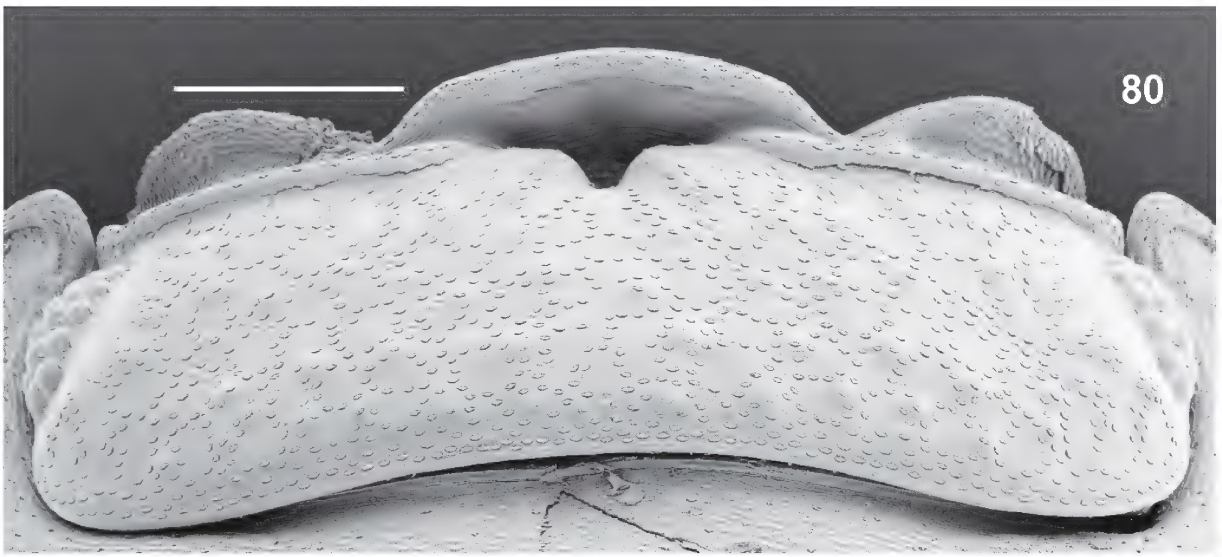
Remarks

The species is very close to the allopatric *A. petralonense*, conspicuous differences in the morphology of the male ischium 7 (see under *petralonense*) plead, however, for a separate species status.

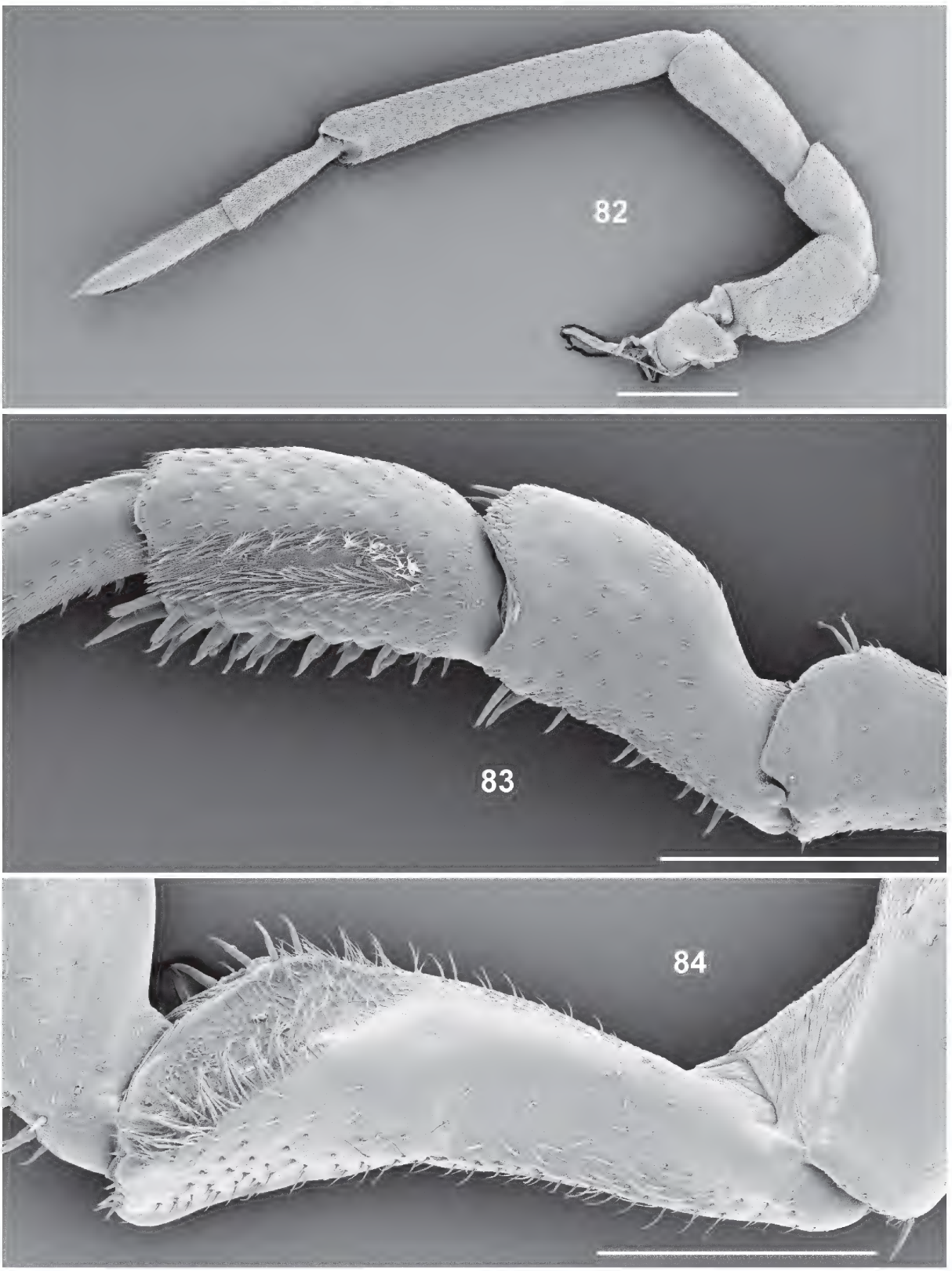
3.12 *Armadillidium sfenthourakisi* **n. sp.**
(Figs. 89–97, map Fig. 88)

Material examined

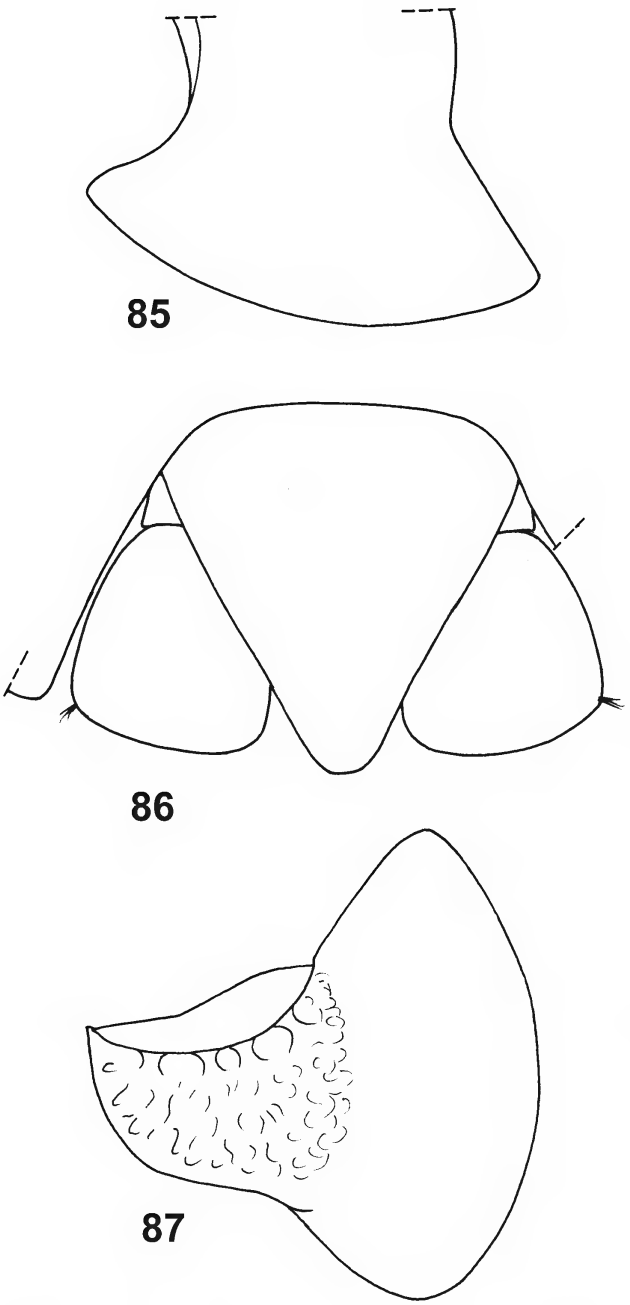
Holotype: ♂, 18.0 × 7.8 mm, Greece, north-central mainland, prefecture Pieria, E of Ólimpos Mountain, Litókhoro, leg. Kühnelt, 1.V.1960 (SMNS T605).



Figs. 80–81. *Armadillidium pieperi* n. sp., paratype from peninsula Kassándra (SMNS 1900). – **80**. ♀, 11.2 × 5.0 mm, head, dorsal view. **81**. ♂, 9.5 × 4.2 mm, head, frontal view. – Scales: 0.5 mm.



Figs. 82–84. *Armadillidium pieperi* n. sp. – **82**. Paratype from peninsula Kassándra (SMNS 1900), 11.2 × 5.0 mm, antenna. **83**. ♂, 12.2 × 5.5 mm, holotype (SMNS T603), pereiopod 1, frontal view. **84**. As before, ischium 7, frontal view. – Scales: 0.5 mm.



Figs. 85–87. *Armadillidium pieperi* n. sp., ♂, 12.2 × 5.5 mm, holotype (SMNS T603). – **85**. Pereion-epimeron 1, lateral view. **86**. Telson and uropods in situ, dorsal view. **87**. Pleopod-exopodite 1, dorsal view.

P a r a t y p e s : 4 ex., same data as holotype (SMNS 1701). – 6 ex., prefecture Pieria, 20 km S of Kateríni, Dío, leg. SCHÖNFELD, 13.VII.2001 (SMNS 2716). – 10 ex., prefecture Pieria, eastern foot of Ólimpos Mountain, maquis, 500 m, leg. SFENTHOURAKIS, 2.VIII.1990 (SMNS 2772). – 2 ex., prefecture Pieria, eastern foot of Ólimpos Mountain, 1500 m, leg. SFENTHOURAKIS, 3.VIII.1990 (SMNS 2308). – 2 ex., prefecture Pieria, Ólimpos Mountain, "Stavros", leg. KÜHNELT, 2.V.1960 (SMNS 1680). – 8 ex., prefecture Pieria, northern foot of Ólimpos Mountain, SW of Fotiná, mixed forest, leg. SCHMALFUSS, 7.VI.1976 (SMNS 1725). – 1 ex., central Greek mainland, prefecture Lárissa, E of Kariá, mixed forest, leg. SCHMALFUSS, 2.VI.1976 (SMNS 1799).

Derivatio nominis

Named after Dr. SPYROS SFENTHOURAKIS (Pátra/Greece), whose detailed investigations led to a first comprehensive overview of the terrestrial isopod fauna of the central Aegean islands and to the discovery of a considerable number of island endemisms.

Diagnostic characters

Maximum dimensions: 17.0 × 6.7 mm.

Coloration: Adult specimens blackish gray, smaller specimens lighter and brownish.

Cuticular structures: Tergites granulated (Fig. 89).

Frontal shield from behind surpassing frontal margin of head, upper margin straight, obtuse angles laterally (Fig. 89); antennal lobes triangular (Fig. 90). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 95). Telson conspicuously longer than wide, with straight sides and broadly rounded apex (Fig. 96). Antenna very slender, segments of the flagellum more or less the same length (Fig. 91). Male carpus 1 with brush of short spines (Fig. 92); male ischium 7 ventrally straight, frontally with distal hair-field (Figs. 93–94). Male pleopod-exopodite 1 with triangular pointed hind-lobe (Fig. 97), endopodite 1 with apex straight.

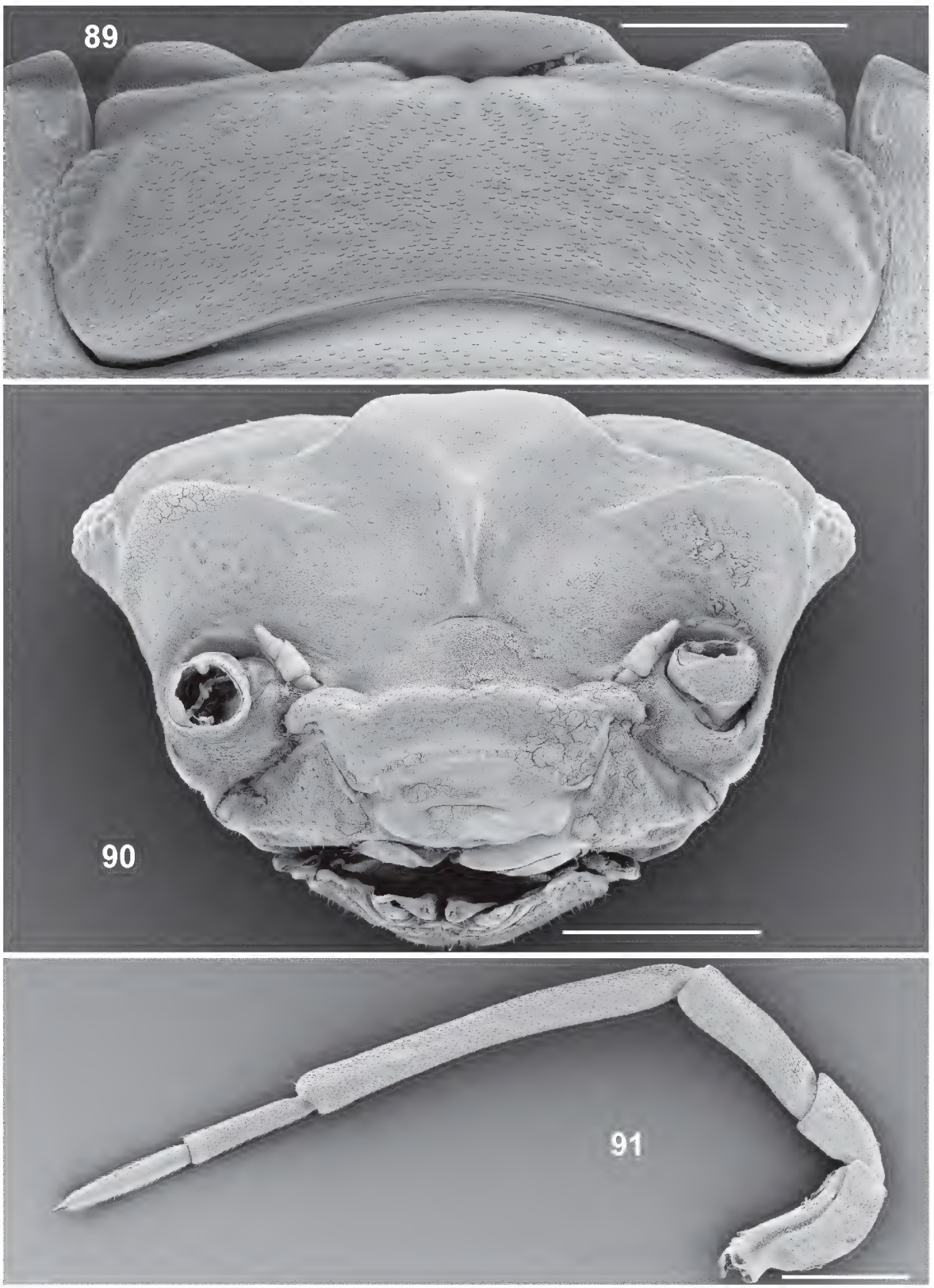
Distribution

North-central Greek mainland, seems to be restricted to the Ólimpos Mountain massive (map Fig. 88).

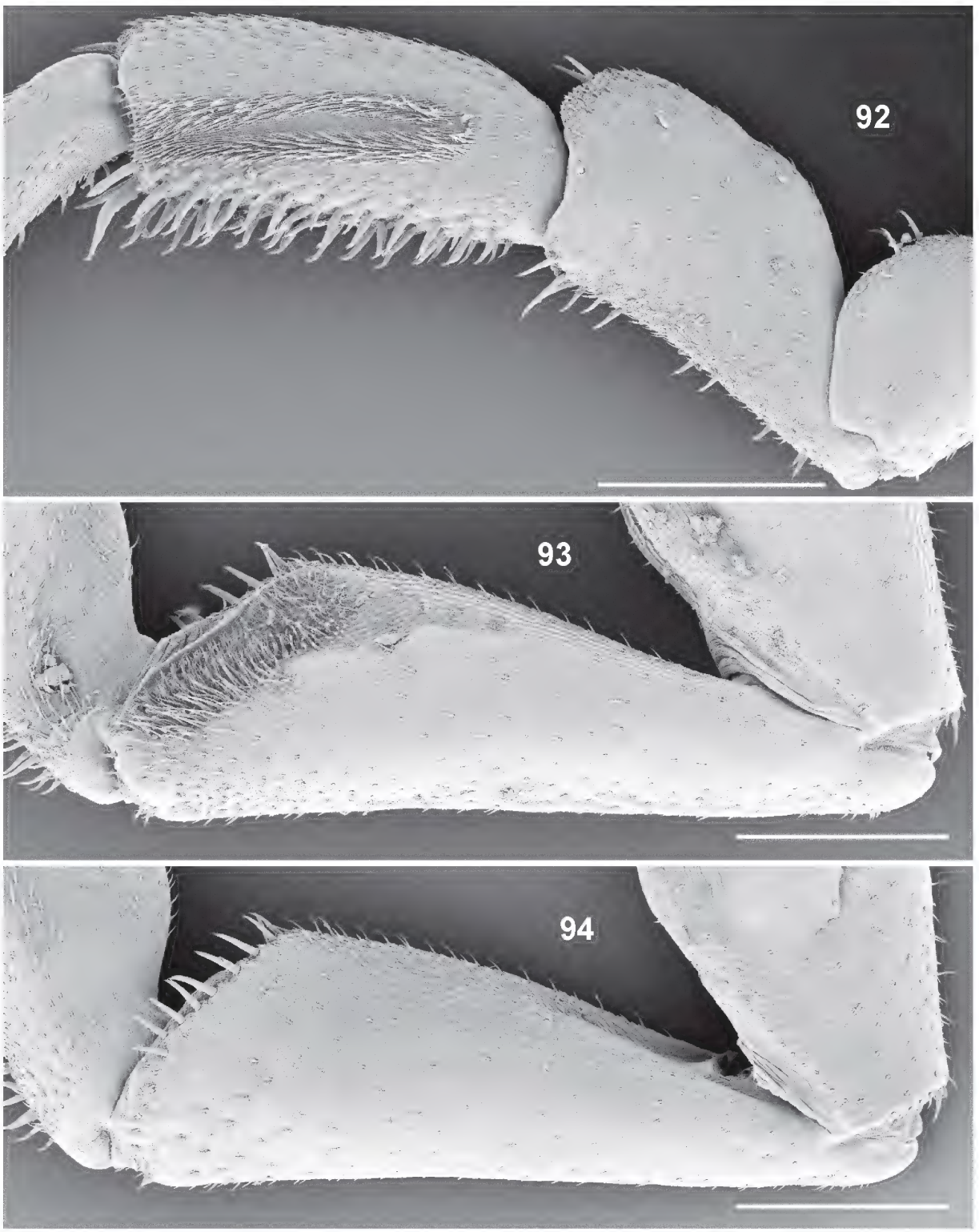
Remarks

This species does not exhibit any clear affinities to other species of the region. Perhaps the next relatives are the species of the *jonicum*-group (*jonicum* and *epiroticum*) from the western part of Greece, but it is only the shape of the telson that points in this direction.

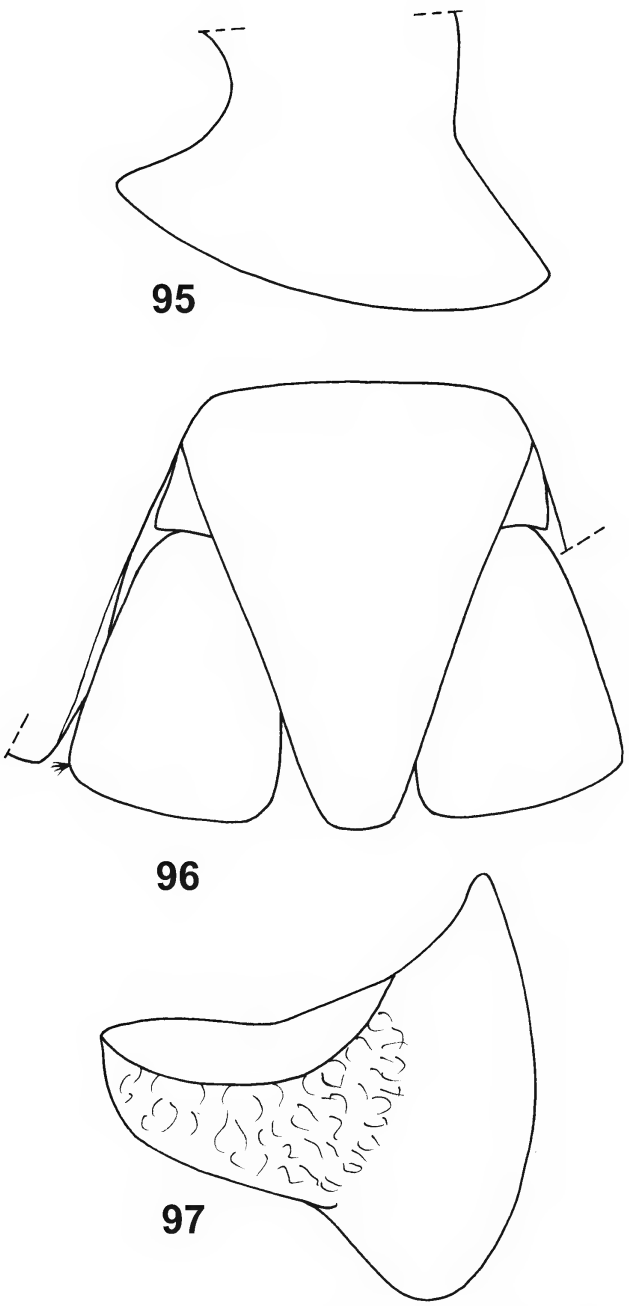
Fig. 88. Known records of *Armadillidium pangaionum* n. sp. (●) and *A. sfenthourakisi* n. sp. (■).



Figs. 89–91. *Armadillidium sfenthourakisi* n. sp., paratypes from type locality (Litókhoro, SMNS 1701). – **89**. ♂, 16.5 × 7.8 mm, head, dorsal view. **90**. ♂, 16.5 × 8.0 mm, head, frontal view. **91**. ♂, 16.5 × 8.0 mm, antenna. – Scales: 1 mm.



Figs. 92–94. *Armadillidium sfenthourakisi* n. sp., paratype from type locality (Litókhoro, SMNS 1701). – **92**. Pereiopod 1, frontal view. **93**. Ischium 7, frontal view. **94**. Ischium 7, caudal view. – Scales: 0.5 mm.



Figs. 95–97. *Armadillidium sfenthourakisi* n. sp., ♂, 18.0 × 7.8 mm, holotype (SMNS T605). – **95**. Pereion-epimeron 1, lateral view. **96**. Telson and uropods in situ, dorsal view. **97**. Pleopod-exopodite 1, dorsal view.

3.13 *Armadillidium tuberculatum* **n. sp.**
(Figs. 98–107, map Fig. 108)

Material examined

Holotype: ♂, 9.0 × 3.8 mm, Greece, northern mainland, prefecture Kavála, SW of Pangéo Mountain, Galipsós, maquis, leg. Schmalfuss, 5.V.1990 (SMNS T604).

Paratypes: 13 ex., same data as holotype (SMNS 2273). – 21 ex., prefecture Kavála, 15 km SW of Kavála, Néa Iraklítsa, beach, leg. Schmalfuss, 5.V.1990 (SMNS 2272). – 3 ex., prefecture Kavála, Pangéo Mountain, southern side, 2 km W of Podokhóri, leg. Pieper, 19.IV.1987 (SMNS 2233). – 8 ex., prefecture Kavála, Pangéo Mountain, southern side, 550 m, maquis, leg. Schmalfuss, 3.V.1990 (SMNS 2276). – 13 ex., prefecture Kavála, 5 km W of Eleftherúpoli, maquis, *Quercus*, *Platanus*, leg. Schmalfuss, 29.IV.1994 (SMNS 2432). – 16 ex., prefecture Kavála, SW of Kavála, Símvolo Mountain, 700 m, maquis, leg. Schmalfuss, 2.V.2002 (SMNS 2734).

Derivatio nominis

The name of the species is derived from the very conspicuous tuberculation of the tergal parts.

Diagnostic characters

Maximum dimensions: 10.0 × 3.8 mm.

Coloration: Tergites light brown, epimera yellowish.

Cuticular structures: Tergites conspicuously tuberculated (Figs. 98, 100).

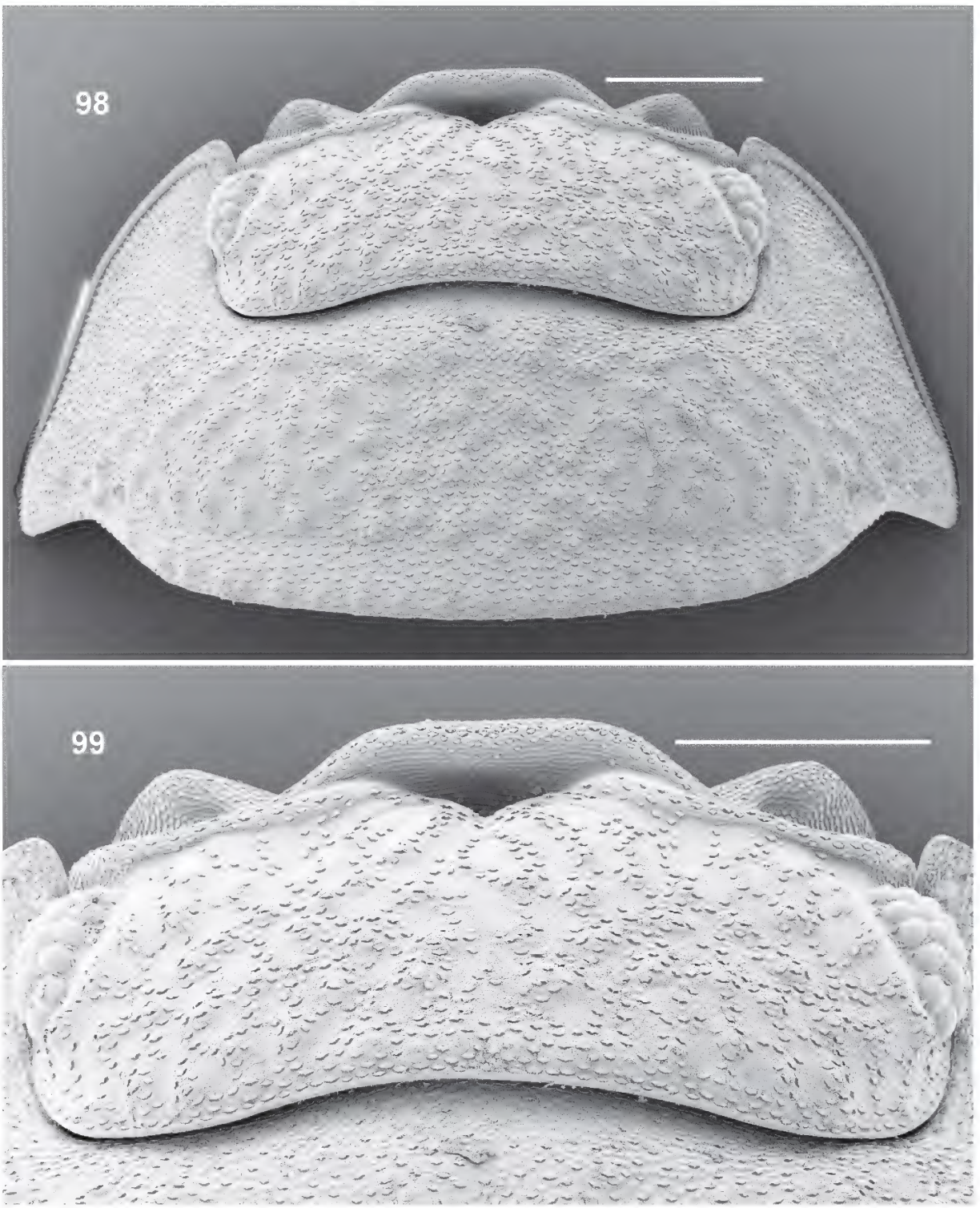
Frontal shield from behind surpassing frontal margin of head, upper margin straight, rounded obtuse angles laterally, caudally with conspicuous groove (Fig. 99); antennal lobes trapezoidal (Fig. 100). Hind margin of pereion-epimeron 1 with obtuse angle (Fig. 105). Telson wider than long, with nearly straight sides and truncate apex (Fig. 106). Antenna see Fig. 101, distal segment of the flagellum slightly longer than proximal one. Male carpus 1 with brush of short spines (Fig. 102); male ischium 7 ventrally very slightly concave, frontally with distal field of tiny setae (Figs. 103–104). Male pleopod-exopodite 1 with short rounded triangular hind-lobe (Fig. 107), endopodite 1 with apex straight.

Distribution

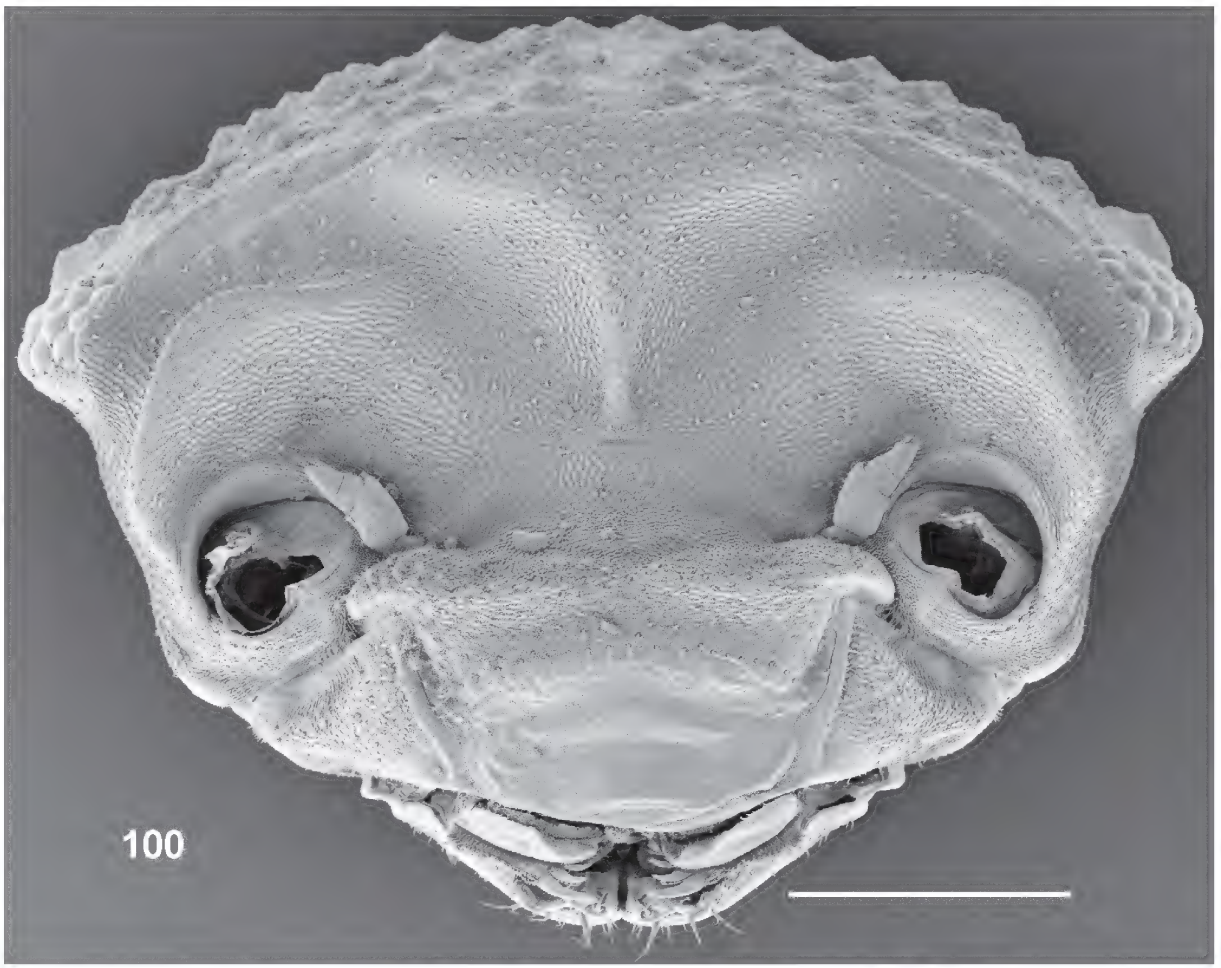
Northern Greece, coastal region in the prefecture Kavála (map Fig. 108).

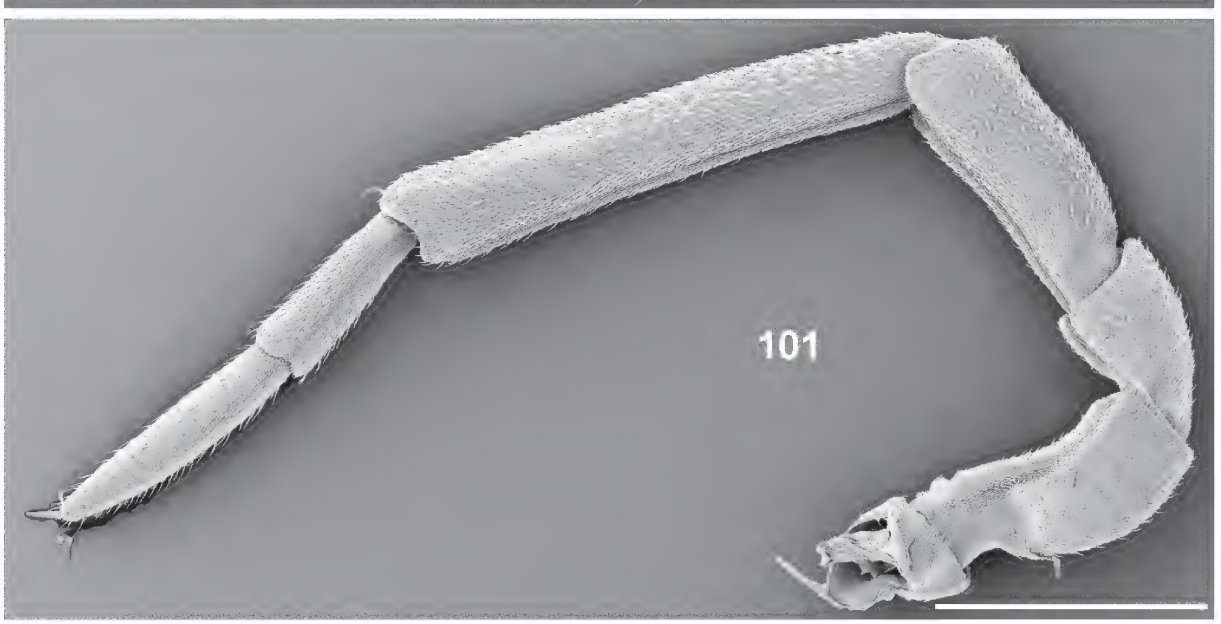
Remarks

The species shows affinities to *A. bicurvatum* and *A. peloponnesiacum* (compare Schmalfuss 2006a). The main differences towards *A. bicurvatum* are: lack of a duplocarinate frons, posterior margin of epimeron 1 with pronounced angle, proximal segment of antennal flagellum two thirds as long as distal segment. *A. peloponnesiacum* exhibits a very different morphology of the male ischium 7 (ventrally strongly concave with a peculiar ventral-proximal scale field, see Schmalfuss 2006a: 77–78, figs. 169–170).

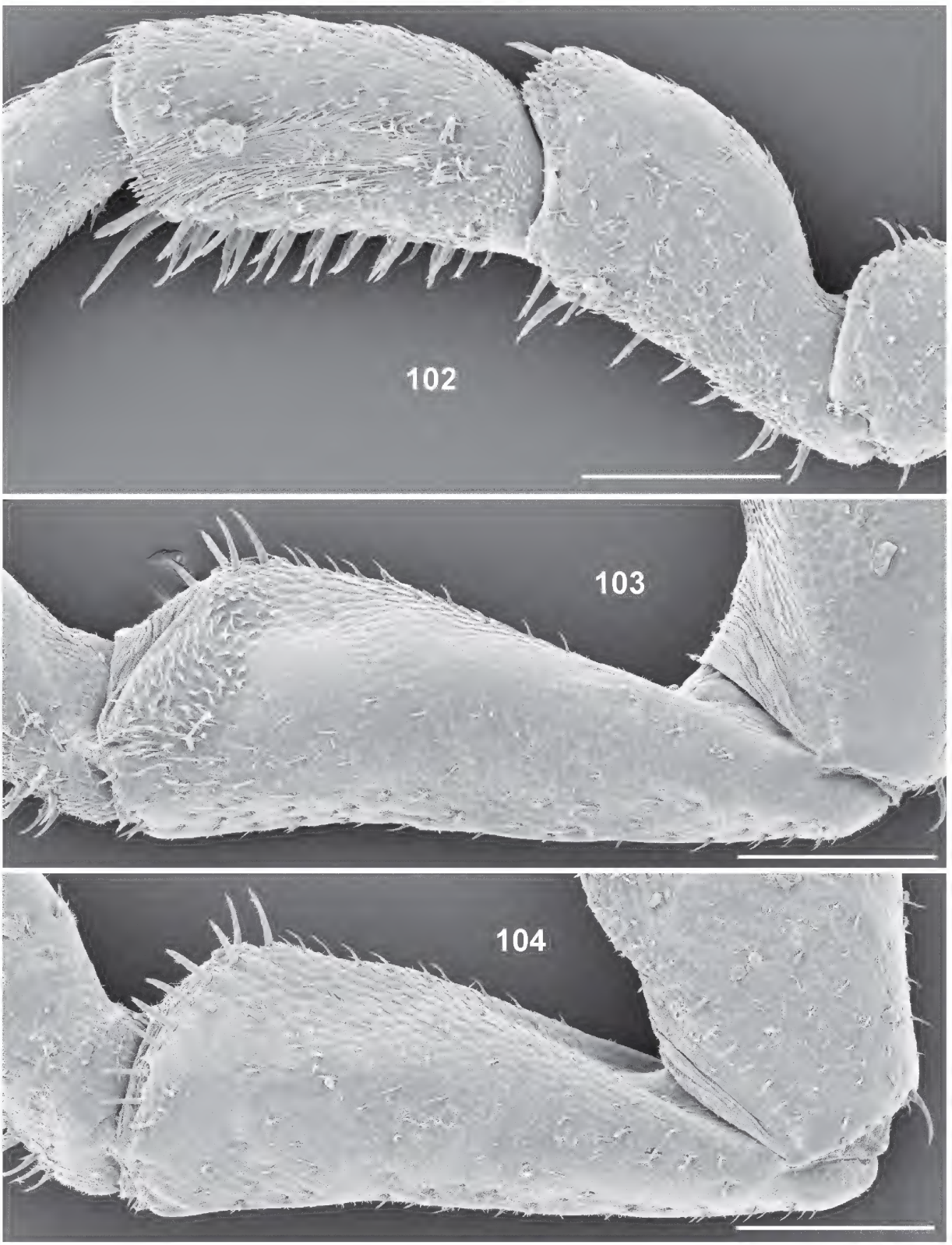


Figs. 98–99. *Armadillidium tuberculatum* n. sp., ♂, 7.8 × 3.5 mm, paratype from type locality (Pangéo Mountain, SMNS 2273). – **98**. Head and pereion-tergite 1, dorsal view. **99**. Head, dorsal view. – Scales: 0.5 mm.

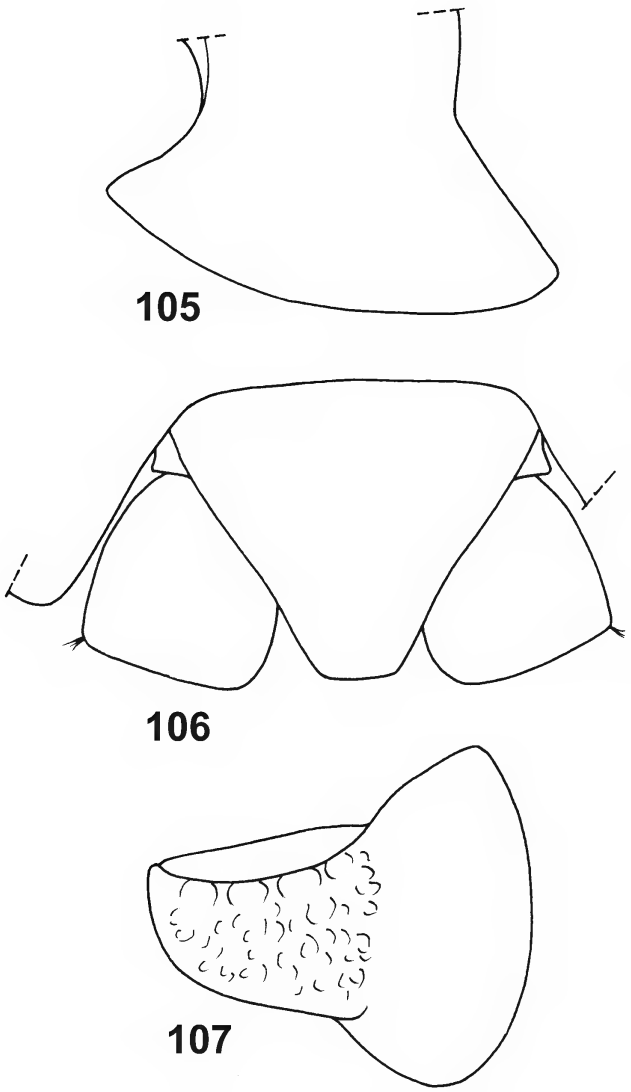




Figs. 100–101. *Armadillidium tuberculatum* n. sp., paratypes from type locality (Pangéo Mountain, SMNS 2273). – **100**. ♀, 10.2 × 4.0 mm, head, frontal view. **101**. ♂, 7.8 × 3.5 mm, antenna. – Scales: 0.5 mm.



Figs. 102–104. *Armadillidium tuberculatum* n. sp., ♂, 7.8 × 3.5 mm, paratype from type locality (Pangéo Mountain, SMNS 2273). – **102**. Pereiopod 1, frontal view. **103**. Ischium 7, frontal view. **104**. Ischium 7, caudal view. – Scales: 0.2 mm.



Figs. 105–107. *Armadillidium tuberculatum* n. sp., ♂, 9.0 × 3.8 mm, holotype (SMNS T604). – **105**. Pereion-epimeron 1, lateral view. **106**. Telson and uropods in situ, dorsal view. **107**. Pleopod-exopodite 1, dorsal view.

3.14 *Armadillidium vulgare* (Latreille, 1804)

This species was again treated in the 23rd contribution of this series (Schmalfuss 2006a). It originated with great probability in southeastern Europe and has been transported by human activities to all parts of the world, where it thrives mostly in disturbed biotopes where the indigenous fauna was destroyed together with the original vegetation for agricultural reasons. A map of all Greek records is given in Schmalfuss (2006a).

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Fig. 108. Known records of *Armadillidium tuberculatum* n. sp.

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Manuscript received: 22.VIII.2007, accepted: 25.IX.2007.

The morphology of the pterothorax of Ephemeroptera, Odonata and Plecoptera (Insecta) and the homology of wing base sclerites and flight muscles[1]

Jana Willkommen

Abstract

The ability to fly was the decisive factor for the evolutionary success of the most diverse group of insects, the Pterygota. Nevertheless, the ground plan of the functionally important wing base has not been sufficiently clarified.

The aim of this study is to homologise the wing base sclerites of Ephemeroptera, usually regarded as sister group of the remaining Pterygota, with that of other basal pterygote lineages and to reconstruct the ground plan of the wing base of Pterygota. The pterothoracic musculature of representatives of the three basal lineages of Pterygota (Ephemeroptera, Odonata and Neoptera) is also described and discussed.

Contrary to previous hypotheses, it is shown that most elements of the neopteran wing base are also present in Ephemeroptera and Odonata. The wing base in the ground plan of Pterygota is presumably composed of three axillary sclerites. The proximal median plate is probably also present in the ground plan of Pterygota. The first axillary is provided with two muscles. The third axillary is equipped with a short muscle that originates from the epimeron. This muscle is interpreted as another ground plan character of Pterygota. In Plecoptera a second muscle inserts at the third axillary sclerite. It originates from the episternum and is most likely an autapomorphic character of Neoptera. The results imply that the wing base of the Plecoptera is close to the pterygote ground plan. It is assumed that the wing base of Ephemeroptera and Odonata is secondarily stiffened. The so-called basalare and its associated muscles in Ephemeroptera and Odonata are probably not homologous to the basalare and respective muscles in Neoptera.

The enlarged subalare and associated muscles, the large dorsal longitudinal muscle, the small metathorax and shortened hind wings in Ephemeroptera suggest that mayflies have a derived flight apparatus in many respects. The Odonata on the other hand show different specialisations, namely a synthorax, large direct flight musculature, and a fusion of second and third axillary with the proximal median plate. Though the wing base in both taxa is secondarily stiffened, the specialisations of Ephemeroptera and Odonata may have evolved independently from each other.

Keywords: Axillaries, subalare, basalare, flight muscles, basal Pterygota, Palaeoptera, Metapterygota.

Zusammenfassung

Die Flugfähigkeit der geflügelten Insekten (Pterygota) war der entscheidende Faktor für den evolutiven Erfolg dieser äußerst artenreichen Gruppe. Dennoch ist der Aufbau des funktionell wichtigen Flügelgelenkes im Grundplan der Pterygota noch nicht zufriedenstellend aufgeklärt.

Ziel dieser Arbeit ist es, die Flügelbasissklerite der Ephemeroptera, gemeinhin als Schwestergruppe der übrigen Pterygota angesehen, mit denen anderer basaler Pterygota zu homologisieren und den Grundplan des Flügelgelenks der Pterygota zu rekonstruieren. Ferner wird die pterothorakale Muskulatur von Vertretern der drei basalen Gruppen der Pterygota (Ephemeroptera, Odonata and Neoptera) beschrieben und diskutiert.

Entgegen früherer Hypothesen sind die Elemente der neopteren Flügelbasis sowohl in der Flügelbasis der Ephemeroptera als auch in jener der Odonata wiederzufinden. Vermutlich ist die Flügelbasis im Grundplan der Fluginsekten aus drei Axillaria aufgebaut. Wahrscheinlich ist auch die proximale Medianplatte im Grundplan der Pterygota vorhanden. Das erste Axillare ist im Grundplan der Pterygota mit zwei Muskeln ausgestattet. Ein weiterer Muskel zieht vom Epimeron zum dritten Axillare. Höchstwahrscheinlich eine Neuerwerbung der Neoptera ist dagegen ein Muskel, welcher bei den Plecoptera vom dritten Axillare zum Episternum zieht. Möglicherweise kommt das Flügelgelenk der Plecoptera dem Grundplan der Flügelbasis der Pterygota sehr nahe. Es wird dagegen angenommen, dass die Flügelbasis der Ephemeroptera und Odonata sekundär versteift ist. Das so genannte Basalare und seine Muskeln der Ephemeroptera und Odonata sind wahrscheinlich nicht mit dem Basalare und den zugehörigen Muskeln der Neoptera homolog.

Das vergrößerte Subalare nebst dazugehörigen Muskeln, der stark vergrößerte dorsale Längsmuskel, der verkleinerte Metathorax und die verkürzten Hinterflügel bei Ephemeropteren legen nahe, dass deren Flugapparat in vielerlei Hinsicht abgeleitet ist. Dagegen besitzen die Odonata andere Spezialisierungen im Pterothorax, beispielsweise einen Synthorax, vergrößerte direkte Flugmuskeln sowie die Verschmelzung des zweiten und dritten Axillare mit der proximalen Medianplatte. Obwohl beide Taxa eine sekundär versteifte Flügelbasis besitzen, sind diese Spezialisierungen bei Ephemeroptera und Odonata wohl unabhängig voneinander entstanden.

[1] Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultäten der Georg-August-Universität zu Göttingen

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1 Introduction

Mayflies (Ephemeroptera) are usually regarded as one of the most ancient extant lineages of winged insects (Pterygota). Among the characteristic features of extant mayflies are the moult of a winged subadult stage (the subimago), short antennae, the costal brace, the reduction of metathorax and hind wings, the medial abdominal terminal filament, and in the male prolonged fore legs, a pair of abdominal claspers and paired penes (Hennig 1969; Kristensen 1975, 1981; Staniczek 2000, 2001; Willmann 2003).

Usually, the adult life span of mayflies is very short lasting from a couple of hours to a few days. Mayflies do not feed in the winged stages, and their mouthparts are atrophied. Due to the short adult life span the emergence of mayflies must be synchronised to ensure mating and reproduction. Male imagines perform characteristic nuptial dances to attract females, and also mating takes place in the air. In several species the female mates as subimago, but in the majority of species mating takes place in the adult stage.

The fossil record (e. g. Grimaldi & Engel 2005, Kluge 1993, McCafferty 1990, Sinitshenkova & Coram 2002, Sinitshenkova 1984, Tshernova 1970) of mayflies dates back to the Permian, although some fossils that are regarded as close relatives [*Lithoneura lameerei* Carpenter, 1938, *Triplosoba pulchella* (Brongniart, 1893)] are recorded from the Carboniferous (Grimaldi & Engel 2005). The position of the Carboniferous taxon *Triplosoba pulchella* is controversial since the characteristic costal brace is absent (Carpenter 1963). There is also no general agreement on the position of *Bojophlebia prokopi* Kukalová-Peck, 1985 and *Lithoneura lameerei* that are regarded as earliest stem group representatives of mayflies by some authors (Carpenter 1987, Grimaldi 2001, Kukalová-Peck 1985, Willmann 1999).

Protereismatoidea, known from the Permian, are generally accepted as stem group representatives of Ephemeroptera. The Protereismatidae are characterised

by fore and hind wings of similar size, though the hind wings are slightly shorter than the fore wings (Carpenter 1979, 1992). The oldest known representative belonging to the extant crown group is the Jurassic *Stackelbergisca sibirica* Tshernova, 1967 (Carpenter 1992, Hubbard 1990, McCafferty 1990, Sinitshenkova 1984), which has been assigned to the Siphluriscidae recently (Zhou & Peters 2003).

The development of wings in insects was one key character for the evolutionary success of this diverse group. It opened up new ecological niches and increased the efficiency of dispersal. The winged insects also take advantage of the flight ability in providing with food and in being able to escape fast from hunters.

Up to date there is no general agreement on the derivation of wings and the evolution of wing base sclerites. The wings are for example assumed to be derivates of the legs (Kukalová-Peck 1983), or derived from paranota, which are lateral expansions of the tergites (Hamilton 1971, 1972a, 1972b, 1972c) or rather originate from both tergites and pleurites (Snodgrass 1935). Also the problem of the wing base ground plan of Pterygota is unsolved. On the one hand it is assumed that the wing base consists of 32 sclerites in the pterygote ground plan (Kukalová-Peck 1983, 1987, 1991). According to this author, these sclerites are secondarily fused in different ways in extant Pterygota. Even up to date it is hypothesised, that Ephemeroptera possess only one axillary plate, Odonata have two axillary plates, and Neoptera possess three axillary plates in the wing base, of which the last mentioned condition represents the apomorphic state (Gullan & Cranston 2005). Also the phylogenetic relationships among the three basal clades of Pterygota remain controversial, in spite of a long history of research into wings and their venation (Bechly 1996, 1999; Comstock 1918; Comstock & Needham 1898, 1899; Edmunds & Traver 1954; Forbes 1943; Hamilton 1971, 1972a, b, c; Kukalová-Peck 1985; Riek & Kukalová-Peck 1984; Wootton 1979, 1992). The first hypothesis (Chiastomyaria hypothesis) assumes a sister group relationship between Odonata and Ephemeroptera+Neoptera (Lemche 1940, Schwanwitsch 1943). The Palaeoptera hypothesis (Martynov 1925) states that Ephemeroptera+Odonata is the sister group to Neoptera, and the Metapterygota hypothesis assumes a sister group relationship between Ephemeroptera and Odonata+Neoptera (Börner 1909; Fürst von Lieven 2000; Hennig 1953; Kristensen 1975, 1981, 1991; Staniczek 2000, 2001).

The musculature and the thoracic sclerites of various insects have been treated in different studies (e. g. Barlet 1967; Crampton 1914, 1918; Maki 1938; Matsuda 1970; Mickoleit 1969; Rähle 1970; Snodgrass 1927, 1935; Weber 1924a, 1924b, 1925). The thoracic musculature and sclerites especially of Ephemeroptera, Odonata and Plecoptera were also examined by various authors (Asahina 1954; Clark 1940; Cremer 1934; Dürken 1907; Grandi 1947; Hatch 1966; Maloeuf 1935; Matsuda 1956; Nelson & Hanson 1968, 1971; Knox 1935; Kluge 1994; Brodsky 1970, 1974, 1979b; Wittig 1955; Pfau 1986; Zwick 1973). Extensive investigations on structure and function of the flight apparatus of insects and insect flight in general were done by Brodsky (1971, 1975, 1986, 1992), who summarised most of the results in a compendium (Brodsky 1994). Other major contributions were published by Dudley (2002), Nachtigall (1966, 1967, 2003), Nachtigall et al. (1998), Wootton & Kukalová-Peck (2000) and Wootton (1979, 1992). The general morphology of mayflies has been treated by Kluge (1994, 2004). Several works dealing with the structure of the wing base and its associated sclerites were done by Brodsky (1970, 1974, 1979a, 1979b), Browne & Scholtz (1994, 1995, 1996), Grandi (1947), Haas & Kukalová-Peck (2001), Hörnschemeyer (1998, 2002, 2004), Ivanov (1995, 1996, 1997), Kukalová-Peck (1974b, 1983), Onesto (1959a, 1959b, 1960, 1961, 1963, 1965), Pfau (1977, 1986, 1991), Sharplin (1963a, 1963b, 1964), Snodgrass (1909), Tannert (1958) and Yoshizawa & Saigusa (2001).

Morphological and molecular investigations and discussions towards the sistergroup relationships among basal Pterygota and Ephemeroptera have been contributed amongst others by Kristensen (1975, 1981, 1991), Ogden & Whiting (2003, 2005), Willmann (1998, 2003, 2005), Whiting et al. (1997), and Wheeler et al. (2001). The Palaeoptera hypothesis is supported on the basis of morphological data for example by Bechly et al. (2001), Gorb et al. (2000), Hennig (1969), and Wagner et al. (1996), and with molecular data by Hovmöller et al. (2002), which is however not clearly supported by Ogden & Whiting (2003). According to Börner (1909), Fürst von Lieven (2000), and Staniczek (2000, 2001) there is evidence for the Metapterygota hypothesis.

There are several different hypotheses on the homology of the wing base sclerites between Ephemeroptera, Odonata and Neoptera (Bekker 1954; Brodsky 1970, 1974, 1994; Grandi 1947; Kluge 1994, 2004; Kukalová-Peck 1974a, 1974b, 1978, 1983, 1985, 1987; Kukalová-Peck & Brauckmann 1990; Matsuda 1956, 1970; Tsui & Peters 1972; for detailed explanations see section 4.2). Some of them are mainly based on topographical characteristics, for example the spatial orientation of the sclerites within the wing base. Others rely on the relative position of the sclerites to each other and to the notal wing processes. Even different works of one and the same author resulted in different hypotheses (Brodsky 1970, 1974). Up to date, no consensus on the different hypotheses was reached so that the problem has to be regarded as unsolved. The aim of the present study is to compare the ephemeropteran wing base with the wing base sclerites of Neoptera, and to reconstruct the wing base ground plan of Pterygota. Previ-

ous hypotheses are discussed and in addition, the pterothoracic musculature is compared.

The Ephemeroptera are often assumed to be the sistergroup of the remaining Pterygota. Consequently, this study focuses on Ephemeroptera. It is complemented by investigations on Odonata and Plecoptera. The latter possibly represent the sister group to the remaining Neoptera or rather the remaining Polyneoptera (Hennig 1969, Kristensen 1991, Zwick 1980), and most likely retained many primitive characters with regard to the wing base.

Acknowledgements

First of all I would like to thank PD. Dr. T. Hörnschemeyer and Prof. Dr. R. Willmann (Göttingen) for their general support and encouragement during the time of my doctoral thesis. Special thanks also to PD. Dr. T. Hörnschemeyer (Göttingen), Dr. G. Bechly (Stuttgart) and Dr. A. Staniczek (Stuttgart) for valuable comments and discussions.

Furthermore, thanks are given to Dr. J. Goebbels and J. Nötel (Berlin) for the acquisition of the µCT data and to B. Wipfler and U. Kalbitzer (Göttingen) for the 3D-reconstruction of the µCT data.

Sincere thanks to Prof. Dr. P. Zwick (Schlitz), Dr. A. Staniczek (Stuttgart), Dr. J.-L. Gattolliat (Lausanne), Dipl. Geol. J. Brinkmann (Tübingen), Dipl. Biol. F. Wieland, Dipl. Biol. O. Eikel, Dipl. Biol. R. Klug and Dipl. Biol. V. Feuerstein (all Göttingen), PD. Dr. T. Hörnschemeyer, Dipl. Biol. U. Griesser (Stuttgart), Dr. A. Golubović (Tübingen), and Dr. M. Ohl (Berlin) for loan and donation of specimens.

I am grateful to J. Reibnitz (Stuttgart) for his valuable advice with colour electronic page setting, and to Dr. E. Weber and Drs. E. and G. Mickoleit (Tübingen) for advice regarding methods.

I owe special thanks to K. Crane (Erlangen) and A. Baxter (Hull) for their help and the corrections of the English language.

This work was supported by a grant to PD. Dr. T. Hörnschemeyer from the Deutsche Forschungsgemeinschaft (DFG HO 2306/2-1, 2-3).

2 Material and Methods

2.1 Materials

The examined material was fixated in 70–80% ethanol. The number of specimens examined is given in square brackets. The list given below includes all examined material, even though it is unquoted in sections 3 and 4.

Ephemeroptera, winged stages

Siphlonuridae

Siphlonurus aestivalis (Eaton, 1903): Switzerland, Vaud, des Monneaux, 29.IV.1994, leg. J.-L. Gattolliat; Germany, Baden-Württemberg, Schwäbisch Gmünd, 20.V.2005, leg. A. Staniczek & M. Pallmann [2 ♂♂, 2 ♀♀ imagines].

Baetidae

Baetis sp.: Germany, Baden-Württemberg, Tübingen, River Neckar, 12.VIII.2003, leg. J. Willkommen [20 ♀♀ imagines and subimagines].

Baetis fuscatus (Linnaeus, 1761): Germany, Baden-Württemberg, Hirschau, River Neckar, 2.X.2004, leg. J. Willkommen [1 ♂ imago; 2 ♂♂ subimagines].

Centroptilum luteolum (Müller, 1776): Germany, Baden-Württemberg, Tübingen, River Neckar, 12.VIII.2003, leg. J. Willkommen [3 ♂♂, 9 ♀♀ imagines and subimagines].

Cloeon dipterum (Linnaeus, 1761): Germany, Bavaria, Würzburg, River Main, 25.VI.2005, leg. J. Willkommen [2 ♂♂, 5 ♀♀ imagines; 1 ♀ subimago].

Leptophlebiidae

Habroleptoides confusa Sartori & Jacob, 1986: Germany, Lower Saxony, Löwenhagen, Nieme creek, 5.VI.2004, leg. J. Willkommen [15 ♂♂♀♀ imagines and subimagines].

Habrophlebia lauta Eaton, 1884: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 10.VI.2004, leg. J. Willkommen [1 ♂, 2 ♀♀ imagines; 3 ♀♀ subimagines].

Paraleptophlebia submarginata (Stevens, 1836): Germany, Baden-Württemberg, Rottenacker, River Danube, 15.V.2004, leg. J. Willkommen [3 ♂♂ subimagines].

Heptageniidae

Ecdyonurus submontanus Landa, 1969: Germany, Baden-Württemberg, Munderkingen, River Danube, 6.VIII.2003, leg. A. Golubović [5 ♂♂, 2 ♀♀ subimagines].

Ecdyonurus venosus (Fabricius, 1775): Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. Willkommen [2 ♂♂ imagines].

Epeorus assimilis Eaton, 1885: Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.VI.2004, leg. J. Willkommen [4 ♂♂ imagines].

Heptagenia coerulans (Rostock, 1878): Germany, Bavaria, Regensburg, 26.VII.2005, leg. U. Griesser [2 ♀♀ subimagines].

Heptagenia sulphurea (Müller, 1776): Germany, Bavaria, Würzburg, River Main, 2.VII.2005, leg. J. Willkommen [8 ♀♀ imagines; 2 ♂♂ subimagines].

Rhithrogena semicolorata (Curtis, 1834): Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 8.V.2004, leg. J. Willkommen [11 ♂♂, 2 ♀♀ imagines].

Ephemerellidae

Serratella ignita (Poda, 1761): Germany, Baden-Württemberg, Munderkingen, River Danube, 6.VIII.2003, leg. A. Golubović; Baden-Württemberg, Tübingen, River Neckar, 19.VII.2003, leg. J. Willkommen; Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. Willkommen [24 ♂♂♀♀ imagines and subimagines].

Ephemeridae

Ephemera danica Müller, 1764: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 10.VI.2004, leg. A. Golubović; Tübingen, River Neckar, 10.VII.2003, leg. J. Willkommen [1 ♂, 2 ♀♀ imagines; 4 ♀♀ subimagines].

Caenidae

Caenis horaria (Linnaeus, 1758): Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 6.VIII.2004, leg. J. Willkommen [1 ♂ imago].

Caenis rivulorum Eaton, 1884: Germany, Baden-Württemberg, Rottenacker, River Danube, 15.V.2004, leg. J. Willkommen [5 ♂♂, 2 ♀♀ imagines; 1 ♀ subimago].

Caenis robusta Eaton, 1884: Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 6.VIII.2004, leg. J. Willkommen [2 ♂♂ imagines].

Polymitarcyidae

Ephoron virgo (Olivier, 1791): Germany, Baden-Württemberg, Neckar-Gmünd, River Neckar, 6.VIII.1994, leg. A. Staniczek; Rhineland-Palatinate, Koblenz, River Rhine, 11.VIII.2004, leg. J. Brinkmann; Bavaria, Würzburg, River Main, 7.VIII.2005, leg. J. Willkommen [9 ♂♂ imagines; 7 ♀♀ subimagines].

Povilla adusta (Navás, 1912): Mali, Niger Basin, River Niger, Gao, 7.IX.1987, leg. J.-M. Elouard [1 ♂ imago].

Euthyplociidae

Exeuthyplocia minima (Ulmer, 1916): Ivory Coast, Cavally Basin, River Cavally, Grié (region Toulepleu), 4.II.1988, leg. J.-M. ELOUARD [2 ♂♂ imagines, 1 ♀].

Oligoneuriidae

Elassoneuria sp.: Madagascar, Mangoro Basin, River Mangoro, Mangoro (pont routier), 2.IV.1992, leg. J.-L. GATTOLLIAT [1 ♂].

Oligoneuriella rhenana (Imhoff, 1852): Germany, Baden-Württemberg, Oberriexingen, Enz River, 10.VIII.1996, leg. A. STANICZEK [1 ♂, 1 ♀].

Palingeniidae

Palingenia longicauda (Olivier, 1791): Hungary, Tisza River, 30.VI.1993, leg. M. SARTORI & L. RUFFIEUX [1 ♂, 1 ♀].

Ephemeroptera, larvae

Heptageniidae

Ecdyonurus submontanus Landa, 1969: Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.V.2004, leg. C. JOACHIM [7 specimens].

Baetidae

Baetis sp.: Germany, Lower Saxony, Goslar, Gose creek, 15.IV.2005, leg. J. WILLKOMMEN [4 specimens].

Plecoptera, adults

Pteronarcyidae

Pteronarcys reticulata Burmeister, 1839: Russia, Russian Far East, Primorje, Orekhovka River near Marevka, trib. Malinovka, 17.VI.1998, leg. P. ZWICK [1 ♂].

Chloroperlidae

Chloroperla susemicheli Zwick, 1967: Italy, Valnontey, 14.IX.2004, leg. J. WILLKOMMEN [1 ♂].

Chloroperla tripunctata Scopoli, 1763: Italy, Valnontey, 14.IX.2004, leg. J. WILLKOMMEN [3 ♂♂].

Siphonoperla torrentium (Pictet, 1841): Germany, Lower Saxony, Löwenhagen, Nieme creek, 2.VI.2004, leg. J. WILLKOMMEN [1 ♂].

Perlodidae

Isoperla grammatica Poda, 1761: Germany, Baden-Württemberg, Bebenhausen, Goldersbach creek, 14.VI.2004, leg. A. GOLUBOVIĆ; Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

Isoperla goertzi Illies, 1952: Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [2 ♂♂, 1 ♀].

Perlodes microcephalus Pictet, 1833: Germany, Lower Saxony, Löwenhagen, Nieme creek, 6.VI.2004, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

Capniidae

Capnia vidua Klapálek, 1904: Germany Lower Saxony, Harz National Park, Torfhaus, Oder creek, 15.IV.2004, leg. A. GOLUBOVIĆ [3 ♂♂].

Taeniopterygidae

Brachyptera seticornis (Klapálek, 1902): Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. J. WILLKOMMEN [3 ♂♂, 2 ♀♀].

Leuctridae

Leuctra hippopus Kempny, 1899: Germany, Lower Saxony, Zorge, Zorge creek, 17.IV.2005, leg. J. WILLKOMMEN [1 ♂, 1 ♀].

Nemouridae

Nemoura cinerea Retzius, 1783: Italy, Bormio, 29.V.2004, leg. J. WILLKOMMEN [1 ♀].

Nemoura cf. *flexuosa* Aubert, 1949: Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. A. GOLUBOVIĆ [1 ♀].

Nemoura marginata (Pictet, 1836): Germany, Lower Saxony, Bösinghausen, 19.V.2004, leg. J. WILLKOMMEN [1 ♀].

Nemoura sp.: Germany, Lower Saxony, Bösinghausen, 19.V.2004, leg. J. WILLKOMMEN [1 ♀].

Protonemoura intricata (Ris, 1902): Germany, Lower Saxony, Goslar, Gose creek, 15.IV.2005, leg. A. GOLUBOVIĆ [1 ♀].

Protonemura meyeri Pictet, 1841: Germany, Lower Saxony, Harz, Hohegeiß, Kunzenbach creek, 17.IV.2005, leg. A. GOLUBOVIĆ [1 ♂].

Plecoptera, larvae

Taeniopterygidae

Brachyptera seticornis (Klapálek, 1902): Germany, Lower Saxony, Zorge creek, 17.IV.2005, leg. A. GOLUBOVIĆ [2 specimens].

Odonata, adults

Aeshnidae

Aeshna mixta Latreille, 1805: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 specimen].

Libellulidae

Sympetrum sanguineum Müller, 1764: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♀].

Sympetrum cf. *striolatum* Müller, 1764: Germany, Brandenburg, Rheinsberg, lake Rheinsberger See, 14.X.07, leg. J. WILLKOMMEN [1 ♂].

Lestidae

Lestes barbarus Fabricius, 1798: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♂].

Sympecma fusca Vander Linden, 1820: Germany, Lower Saxony, Pevestorf (Lüchow-Dannenberg), River Elbe, 8.V.2005, leg. T. HÖRNSCHEMEYER [1 ♂].

2.2 Methods

The majority of the specimens was collected into 80% ethanol. Several specimens were first fixated in Duboscq-Brasil (ROMEIS 1989) and after 24 h transferred to 80% ethanol. A few species were fixated in a solution of 95% ethanol, formaldehyde and acetic acid (66 : 33 : 10) and after at least 24 h transferred into 80% ethanol. The examination of dry specimens is not satisfactory, so no dry museum material was used for this study.

Specimens were examined and dissected under a Leica MZ16 stereomicroscope. The muscular preparation was done after cutting specimens sagitally into two halves with a razor blade, while the specimens were fixed onto a prepared cork. Afterwards the halves were each fixed by micro needles in a Petri dish. The thoracic muscles were successively removed from medial to lateral using a pair of Dumont forceps. A few species were dissected after a horizontal cut. The drawings were made using a drawing tube on a Leica MZ16 stereomicroscope.

To examine the thoracic sclerites, some of the specimens were first gradually transferred into 10% ethanol and thereafter to 5% potassium hydroxide solution at room temperature for one to three days until the soft tissues dissolved. Small or fragile specimens were transferred into 15% ethanol for about eight days. After rinsing with distilled water, the cleared specimens were again gradually transferred into 80% ethanol for further examination of the sclerites.

Specimens used for scanning electron microscopy (SEM) were gradually transferred into 100% ethanol and then dried in a Balzer CPD 030 critical point dryer. The dry specimens were sputter-coated with gold (Balzers SCD050 Sputter Coater). The examination and photographs were made with a Leo 438VP scanning electron microscope.

Species with only limited material available were investigated by high resolution X-ray tomography (µCT) at the Federal Institute for Materials Research and Testing, Berlin (BAM) (Hörnschemeyer et al. 2002, Hörnschemeyer 2004). These specimens were prepared in the same way as those used for SEM investigation except of additional cutting off abdomen, wings, and partly the head of the specimens. The dry specimens were fixed vertically (head upwards) on a rivet with paraffin or Leit-C (usually used for SEM). Some of these specimens were sputter coated for subsequent scanning electron microscopy after examination with µCT.

The photographs (except Figs. 58–60) were made with a Nikon Coolpix camera that was mounted on the stereomicroscope. The pictures 58–60 were made with a Leica Macroscope and processed with Synchroscopy Automontage.

Terminology

Terms with "II" or "III" indicate mesothoracic (II) or metathoracic (III) elements. The term "basal plate" (BP sensu Kluge 2000) is equivalent to the term "median plate" (sensu Tsui & Peters 1972) and both terms are used in section 4.2.

The terminology of muscles and sclerites of Ephemeroptera primarily follows Kluge (1994, 2004). For comparison, the terminology used by other authors is given in Tab. 1. The dorsal muscle "t13" is not treated by Kluge, so the terminology of Brodsky (1994) has been used.

The nomenclature of muscles and sclerites of Odonata primarily follows Asahina (1954) and that of the Plecoptera follows Wittig (1955) and Zwick (1973).

For the most part the discussion (section 4.3) is restricted to the mesothoracic muscles since the metathorax and consequently the metathoracic muscles of Ephemeroptera are reduced whereas the flight muscles and the sclerites of Plecoptera are similar in the mesothorax and in the metathorax.

Since the interpretation of the homologies between the ephemeropteran wing base sclerites and the neopteran axillary sclerites is inconsistent within different papers (e. g. Brodsky

Tab. 1. Comparison of ephemeropteran muscles and terminology used by different authors with the homology partly used by Matsuda (1970).

Muscle attachments	Kluge 1994 and this study	Brodsky 1974	Matsuda 1970	Wittig 1955	Maki 1938	Tsui & Peters 1972
phragma I–phragma II	MT.m	Tm1	t 14	dlm 35	20	II-1
scutum–postnotum	S.LPNm	Tm2	t 12	dlm 36	21	II-4
scutum–postnotum		Tm3	t 13	dlm 37	–	–
scutum–episternum	S.ESm	TPm1	t-p 5, 6	dvm 40	25	II-6
scutum–trochantinus			t-ti 2	dvm 41		
scutum–Cx anterior	S.CmA	TCxm1	t-ti 3		36	II-11
scutum–trochanter	S.Trm	TTrm1	t-tr 1	dvm 42		II-14
scutum–Cx posterior	S.CmP	TCxm2/3	t-cx 7	dvm 43	39	II-19
scutellum–Cx posterior	PSL.Cm	TCxm4	t-cx 6	–	40	II-21
notum–pleurum	AN.Pm	TPm6	t-p 3	tpm 46a		II-7
subtegula–episternum			t-p 4	tpm 47		
scutum–episternum			t-p 7	tpm 46b		
ANP–episternum	SrA.Pm	TPm2	t-p 8			II-13?
scutum (PNP)–pleurum			t-p 15	tpm 49		
episternum–Cx anterior	P.Cm		p-cx 5	cpm 52		II-15
episternum–trochanter	P.Trm		p-tr 1			II-16
left mesofurca–right mesofurca	Fm		s 16		23	II-29
profurca–mesofurca	iFm		s 13	vlm 38	22	II-3
furca–Cx anterior	F.CmA		s-cx 5			
furca–Cx posterior	F.CmP		s-cx 2			II-26?
"BA"–sternum	BA.SmS	TSm1	p-s 12		33	II-8
"BA"–sternum	BA.SmI	TSm2	p-s 12		34	II-9
notum–pleurum	BA.Pm	TPm3	p 4, t-p 4	tpm 47	30	II-10
BA–coxa	BA.Cm	TCxm5	t-cx 4	cpm 51	31	II-18
BA–trochanter	BA.Trm	TTrm2	p-tr 2	cpm 50		–
SA–furcasternum	SA.Sm	TSm3	t-s 5		26	II-5
SA–furca	SA.Fm	TSm4	t-s 4		27	II-20
SA–coxa	SA.Cm	TCxm6/7	t-cx 8	cpm 53	41	II-22/II-23
posterior SA–pleurum	–	–	t-p 16	ppm 56	–	–
1Ax–pleurum	Ax.PmI	TPm4	t-p 11		–	–
1Ax–furca	Ax.Fm	TSm5	t-s 3		28	II-17
3Ax–epimeron	Ax.PmS	TPm5	t-p 14		32	II-22a
3Ax–episternum			t-p 13	tpm 48		

1970, 1974; GRANDI 1947; KLUGE 1994, 2004; KUKALOVÁ-PECK 1983, 1985; MATSUDA 1956) it necessitates simplification. Therefore, the wing base sclerites of Ephemeroptera are named first, second, third and fifth sclerite (s1, s2, s3 and s5). Their homology will be discussed later.

In this work the terminology of the wing base sclerites of Odonata follows ASAHINA (1954). The terminology of the wing veins follows RIEK & KUKALOVÁ-PECK (1984). The numbers and the terminology of the odonatan muscles follow ASAHINA (1954). The parenthesised numbers refer to the metathoracic muscles.

The arrangement of the mayfly musculature in the descriptions (and in Tabs. 1, 3) is as follows: Dorsal muscles (dorsal longitudinal, tergal muscles) – dorso-ventral muscles (tergo-pleural muscles) – pleural muscles – ventral muscles – direct flight muscles. The musculature of Odonata is described in ascending order (muscle 21 to muscle 41) with the terminology following ASAHINA (1954). The stonefly muscles are arranged according to ZWICK (1973): Dorsal muscles (dorsal longitudinal muscles) – dorso-ventral muscles (tergo-sternal muscles, tergo-coxal muscles) – pleural muscles (tergo-pleural muscles, pleuro-coxal muscles, direct flight muscles).

Unless otherwise noted, the head is directed to the top in figures in dorsal view, and to the left in figures in lateral view.

The total length of the specimens is measured from the anterior margin of the head (without antennae) to the end of the abdomen (without cerci).

Abbreviations

A	anal vein
A1	anterior anal vein
ab	anal brace
AEM	anepimeron
AES	anepisternum
ALSC	antero-lateral scutal costa
ANi	anteronotal transverse impression
ANP	anterior notal wing process
ANp	anteronotal protuberance
AN.Pm	anteronoto-pleural muscle
ASA	anterior subalar apodeme
AS I	abdominal sternite I
Ax	axillary sclerite (1Ax, 2Ax, 3Ax = first, second, third axillary sclerite)
AxC	axillary cord
Ax.Fm	axillar-furcal muscle
axp	axillary plate (Odonata)
Ax.PmI	inferior axillar-pleural muscle
Ax.PmS	superior axillar-pleural muscle
BA	basalare
BA.Cm	basalar-coxal muscle
ban	basanale
BA.Pm	basalar-pleural muscle
BA.SmI	inferior basalar-sternal muscle
BA.SmS	superior basalar-sternal muscle
BA.Trm	basalar-trochanteral muscle
BP	basal plate
BPp	ventral process of basal plate
BS	basisternum
BSc	basisubcostale
C	costal vein
cb	costal brace
Cu	cubital vein
CuA	anterior cubital vein
CuP	sector of the cubital vein
Cx	coxa (Cx II = coxa of mesothorax; Cx III = coxa of metathorax)
Cx.Cxm	coxo-coxal muscle
DMP	distal median plate
EM	epimeron
ES	episternum
F	furca
F.CmA	anterior furco-coxal muscle
F.CmP	posterior furco-coxal muscle
Fm	furcal muscle
FS	furcasternum
fwp	wing pad of the mesothorax
HP	humeral plate
hp	humeral plate (Odonata)
hwp	wing pad of the metathorax
iFm	intersegmental furcal muscle
KEM	katepimeron
KES	katepisternum
LPN	lateropostnotum
LPNC	lateropostnotal crest
LPs	lateroparapsidal suture
MA	anterior medial vein
MLs	median longitudinal suture
MNP	median notal wing process
MNs	mesonotal suture
MP	posterior medial vein
MPs	medioparapsidal suture
MTm	median tergal muscle
PAB	prealar bridge
P.Cm	pleuro-coxal muscle
PCxsA	anterior paracoxal suture
PCxsP	posterior paracoxal suture
PES	preepisternum
PLs	pleural suture
PLsI	inferior pleural suture
PLsS	superior pleural suture
PMP	proximal median plate
PNP	posterior notal wing process
PRS	prescutum
PSA	posterior subalar apodeme
PSL.Cm	parascutello-coxal muscle
PSp	posterior scutal protuberance
PST	presternite
P.Trm	pleuro-trochanteral muscle
PWP	pleural wing process
R	(anterior) radial vein
Rs	radial sector
RSSs	recurrent scuto-scutellar suture
S	spiracle
s1, s2, s3, s5	wing base sclerites 1–3, 5
S III	sternum III (sternum of the metathorax)
SA	subalare
SA.Cm	subalar-coxal muscle
SA.Fm	subalar-furcal muscle
SAs	subalar suture
SA.Sm	subalar-sternal muscle
Sc	subcostal vein
S.CmA	anterior scuto-coxal muscle
S.CmP	posterior scuto-coxal muscle
Sct	scutum
S.ESm	scuto-episternal muscle
SL	scutellum
SLS	sublateroscutum
S.LPNm	scuto-lateropostnotal muscle
SrA	suralare
SrA.Pm	suralar-pleural muscle
S.Trm	scuto-trochanteral muscle
T	tegula
Tn	trochantinus

3 Results

3.1 General Remarks

In the following, descriptions of pleurum, tergum and muscles of the pterothorax of three species of Ephemeroptera and one species of Odonata are given exemplarily. Additionally, the morphology of tergum and pleurum of the pterothorax of *Pteronarcys* and the muscles of *Brachyptera* (Plecoptera) are described.

Siphlonurus aestivalis (Siphlonuridae), as a rather primordial mayfly (Kluge et al. 1995) shows plesiomorphic conditions in several respects, whereas *Baetis* sp. (Baetidae), even though also rather primitive among the Ephemeroptera with respect to other morphological features, is characterised by very short and rudimentary hind wings. *Ephoron virgo* (Polymitarcyidae) is an example for a more specialised ephemeropteran taxon, which is characterised by horizontal nuptial dances (Brodsky 1973, Fischer 1991).

These investigations are supplemented by a description of a late larva of *Baetis* sp. Additionally, the flight muscles of *Sympetrum* cf. *striolatum* (Libellulidae) are described as an example of Odonata. *Pteronarcys reticulata* (Plecoptera) is a subordinate species among Pteronarcyidae but rather basal among Systellognatha. *Brachyptera seticornis* (Taeniopterygidae) is a basal taxon among Nemouroidea and the remaining Euholognatha.

3.2 Ephemeroptera

3.2.1 General Remarks

The mesothorax of subimaginal and imaginal Ephemeroptera is always larger and more developed than the metathorax. The sutures and sclerites are more distinct, the wings are larger and the flight muscles are much stronger in the mesothorax when compared to the metathorax. The pleurum in Ephemeroptera is less robust than in Plecoptera and other Pterygota because the sclerites are well separated by comparatively large membranous areas.

The hind wings are only about half as long as the fore wings and, in flight, they are often coupled with the fore wings. As a consequence, the metathorax is comparatively short and most of the muscles are considerably smaller than the muscles of the mesothorax. The basalare and the subalare, the fulcrum and most sutures are inconspicuous in the metathorax. In the mesothorax, however, they are all well developed.

Even though the hind and fore wings are coupled in flight, the direct flight muscles are present in the mesothorax and in the metathorax, although they are comparatively smaller in the metathorax.

The diminished size of the metathorax brings about the shortening of the tergal elements, especially of the scutum. The sutures, concavities and convexities that are distinct in the mesotergum are missing in the metatergum.

The superior axillar-pleural muscle (Ax.PmS) running from the third wing base sclerite to the pleurum is visible only if the specimen is dissected with the wings held down.

3.2.2 *Siphlonurus aestivalis*, winged stages (Figs. 1–25) (n = 4)

Measurements

Total length: 15.8 mm (♂), 22 mm (♀). – Length of mesothorax: 4.2 mm. – Length of mesothoracic wing: 14.7 mm (♂), 20.8 mm (♀). – Width of mesothoracic wing: 5 mm (♂), 7.5 mm (♀). – Length of metathorax: 1.35 mm. – Length of metathoracic wing: 6.6 mm (♂), 10.25 mm (♀). – Width of metathoracic wing (measured at the tornus): 3.3 mm (♂), 4.8 mm (♀). – Height of mesothorax: 4.2 mm (2.1 mm belong to MTm). – Height of metathorax: 2.38 mm.

External morphology of the mesonotum

The tergum is subdivided into the notum and postnotum. The notum is subdivided into the prescutum, scutum and scutellum (SL; Figs. 1, 3, 12). The narrow acrotergite and the anterior phragma at the front of the mesonotum separate the prothorax from the mesothorax.

The narrow prescutum has conspicuous lateral arms, which form the prealar bridge (PAB; Figs. 4, 5). The prealar bridge of the mesothorax is subdivided into three arcs. The dorsal arc is extended ventrally and is connected to the ventral arc. The posterior arc is long and ends next to the sclerite where the basalar-pleural muscle is attached (BA.Pm sensu Kluge 1994). The large scutum, posterior to the prescutum, is divided into several concave and convex areas that also serve as the attachment points of the dorso-ventral muscles. The anterior convexity is the anteronotal protuberance (ANp; Fig. 1), which posteriorly ends in the anteronotal impression (ANi; Fig. 1). The prominent and paired posterior scutal protuberances (PSp; Figs. 1–3, 12) are the dorsal attachments of the scutolateropostnotal muscles (S.LPNm; Figs. 15, 16). Posteromedial to the PSp lies the scutellum (SL; Figs. 1–3, 12). The lateral parts of the scutellum are well developed.

The median longitudinal suture (MLs; Figs. 1–3) is clearly visible from the anterior part of the scutum (from the ANi) and it obliterates towards the posterior third of the scutum, well before the PSp. The medioparapsidal sutures (MPs; Figs. 1–3) lateral to the MLs are rather inconspicuous. The lateroparapsidal sutures (LPs; Figs. 1–3) are located lateral to the MPs. They are conspicuous sutures in *S. aestivalis* and disappear at their postero-dorsal end. The conspicuous antero-lateral scutal costa (ALSC; Fig. 1) is located anterior to the lateroparapsidal sutures.

The mesonotal suture (MNs; Figs. 1–3, 8) proceeds across the anterior fourth of the scutum. It is a distinct suture with a carinate anterior rim.

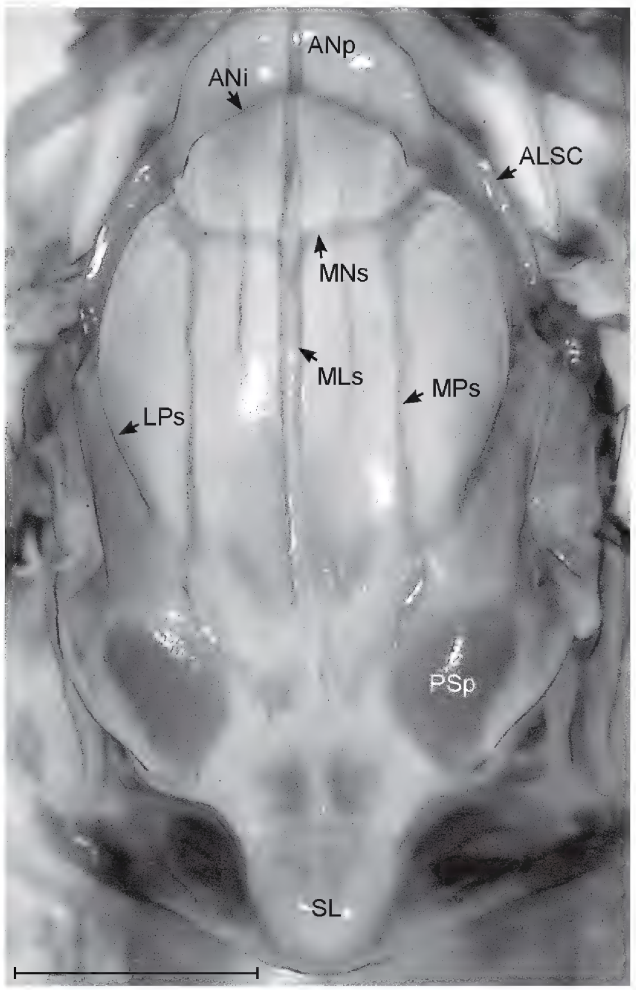


Fig. 1. *Siphlonurus aestivalis*, ♀ imago, mesotergum. – Scale: 1 mm.

Siphlonurus aestivalis has conspicuous anterior and posterior notal wing processes (ANP, PNP; Figs. 2, 3). The anterior notal wing process is long and narrow and is located in direct proximity of the first free wing base sclerite (s1; Figs. 2, 3). The posterior notal wing process is a little less distinct than the anterior one and articulates with the third free wing base sclerite (s3; Figs. 2, 3).

The tegula (T; Figs. 2, 8, 12) is a well separated sclerite, which is located at the anterior base of the wing. Usually, it lacks setae in the imago, but in some male imagines it is sparsely covered with short setae.

Between the tegula and the tergum there are two sclerites. The anterior sclerite is connected to the crescent-shaped sclerite (BA; Figs. 4–8). It is the dorsal point of attachment of the basalar-pleural muscle (BA.Pm sensu Kluge 1994; Figs. 18, 19). The posterior sclerite is the dorsal point of attachment of the basalar-coxal muscle (BA.Cm sensu Kluge 1994; Figs. 17–19). The slightly triangular humeral plate (HP; Fig. 8) is distinct in the fore wing. Its anterior tip is well sclerotised.

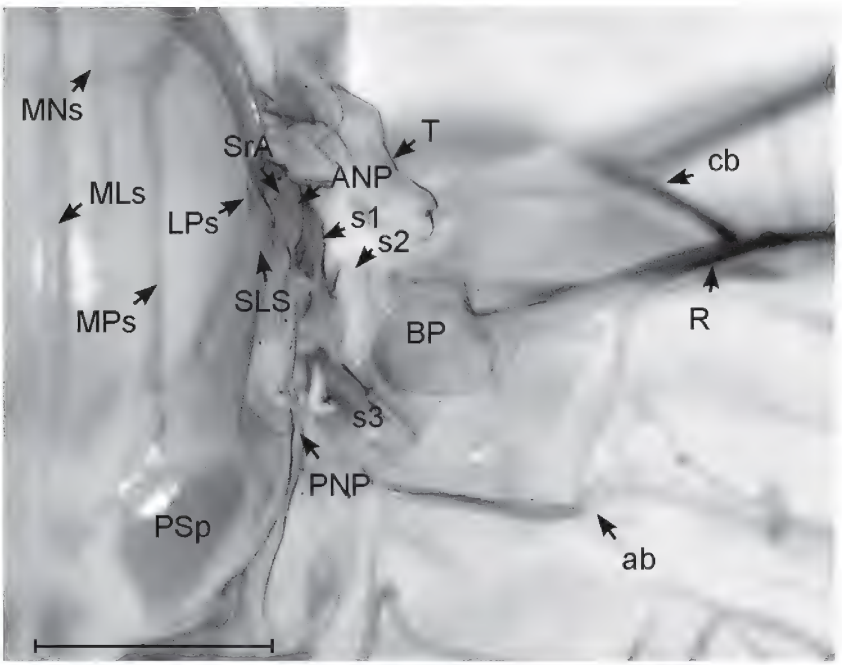
The basal plate (BP; Figs. 2, 3) is a very prominent structure in the wing base. It is sclerotised in both dorsal and ventral layer of the wing membrane. The subcostal vein originates on the antero-ventral side of the basal plate. The radial vein originates almost centrally on the dorsal side of the basal plate. The main part of the BP resembles a convex hemisphere as seen from above. Its postero-medial part is, however, concave with a distinct and well sclerotised posterior edge, which articulates with the s3. The basal part of the BP is flat and anteriorly tapers off into a ventral process (BPp; Fig. 7). This process articulates with the pleural wing process (PWP; Figs. 4–8).

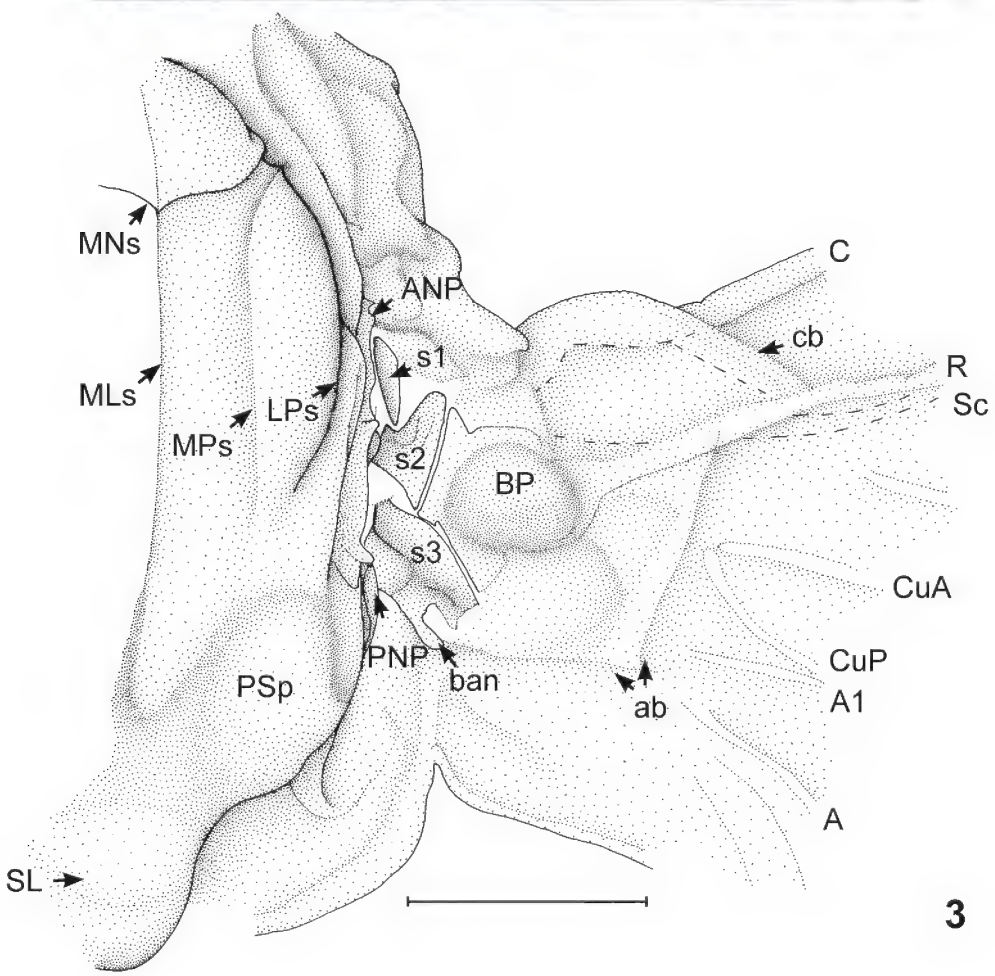
In addition to the basal plate, there are three more sclerites in the wing base. The first free sclerite (s1; Figs. 2, 3) lies distal to the ANP. It articulates distally with the second free wing base sclerite (s2; Figs. 2, 3). The first free sclerite is triangular in shape and narrow. It is only sclerotised in the dorsal layer of the wing membrane. The second free wing base sclerite (s2; Figs. 2, 3) is a distinct, and large sclerite, which is also only sclerotised in the dorsal layer of the wing membrane. The articulation point with the s1 is well sclerotised. The proximal part of s2 is bent inwards. The s2 articulates distally with the basal plate and posteriorly with the third free wing base sclerite (s3; Figs. 2, 3).

The third free wing base sclerite (s3) is a large sclerite, which is not easily distinguishable from the basanale (ban; Fig. 3). It is sclerotised in the dorsal as well as in the ventral layer of the wing membrane. The antero-lateral ridge of the s3 is connected to the posterior rim of the basal plate. The proximal part of s3 articulates with the posterior notal wing process (PNP). Ventrally, the s3 is connected to the subalare (SA; Figs. 5, 10). A fifth, slightly crescent-shaped sclerite is present in the mesothorax (s5, not pictured, compare Fig. 86), which is associated with the scutum between the ANP and PNP.

The wing veins are not directly connected to the wing base sclerites. The s2 is connected to the subcostal vein (Sc; Fig. 3) via the anterior point of the basal plate. The s3 is connected to the anal veins (A; Fig. 3) via the basanale and the anal brace (ab; Figs. 2, 3).

The prominent costal brace (cb; Figs. 2, 3) at the anterior wing base stretches between the costal vein and the anterior radial vein. The costal brace tapers off into a fold, which ends anterior to the BP. In addition, the costal brace is weakly connected to the subcostal vein, near the connection to the radial vein. The proximal (or posterior) arc of the anal brace (ab; Fig. 2) is conspicuous and the distal (or anterior) arc is rather less distinct. The basanale is well sclerotised and distinct in the wing base of *Siphlonurus aestivalis*.





Figs. 2–3. *Siphlonurus aestivalis*, ♀ imago, right fore wing. – Scales: 1 mm.

The radial sector (Rs) is basally fused to the anterior medial vein (MA). The anterior medial vein (MA) and the posterior medial vein (MP) are fused to each other at their bases. The radial sector (Rs) branches off from the MA distal to the MA-MP fork. The distinct anal brace is located between the anterior radial vein and the sclerotised basanale (ban).

The lateropostnotum (LPN, postalar bridge; Figs. 4, 5, 8), which is the ventral point of attachment of the scuto-lateropostnotal muscle (S.LPNm; Figs. 15, 16), is distinct and the lateropostnotal crest (LPNC; Fig. 8) is rather inconspicuous in *Siphlonurus aestivalis*.

External morphology of the mesopleurum (Figs. 4–10, 13)

The most distinct sutures in the mesopleurum are the pleural suture (PLs) and the anterior paracoxal suture (PCxsA; Figs. 4, 5, 8). The pleural suture divides the pleurum into the anterior episternum and the posterior epimeron. The pleural suture is divided into the upper or superior part (PLsS; Figs. 4, 5, 8) and the lower or inferior part (PLsI; Figs. 4, 5, 8). The pleural suture runs almost vertically and extends dorsally into the distinct pleural wing process (PWP; Figs. 4–8). The externally visible condylus of the PWP is rather small. The fulcrum articulates with the ventral process of the basal plate (BPp; Figs. 7, 8). Ventrally, the pleural suture ends at the point where the coxa articulates with the pleurum, the coxo-pleural joint.

The second distinct suture, i. e. the paracoxal suture, is subdivided into the anterior paracoxal suture (PCxsA) and the posterior paracoxal suture (PCxsP; Figs. 5, 8). The anterior suture (PCxsA) is conspicuous, while the posterior suture (PCxsP) is rather inconspicuous. The PCxsA divides the pleurum into a broad anepisternum (AES; Figs. 4, 5, 8) and a narrow katepisternum (KES; Figs. 4, 5, 8). The PCxsP is more distinct in male specimens than in female ones. It divides the dorsal anepimeron (AEM; Fig. 5) from the ventral katepimeron (KEM; Fig. 5).

The basalare (BA; Figs. 4–8) is located anterior to the PWP at the anterior base of the wing. It is a crescent-shaped sclerite, which merges posteriorly with the tegula and dorsally with the tergum. Posterior to the PWP lies the subalare (SA; Figs. 5, 10). It is a conspicuous element of the mesopleurum. Its dorsal part is less sclerotised and less pigmented than the ventral part. The latter is of triangular shape. Its dorsal margin forms a distinct suture (SAs; Fig. 8) that separates the dorsal and ventral part of the subalare from each other. The posterior end of the ventral sclerite forms the large posterior subalar apodeme (PSA; Figs. 4–8). The small anterior subalar apodeme (ASA; Figs. 4–8) is mainly formed by the anterior end of the dorsal subalare. The posterior subalar apodeme and the ventral sclerite of the SA is the area of insertion of the subalar-sternal muscle (SA.Sm; Figs. 14–16). The anterior margin of the dorsal subalare is well sclerotised. The ASA is the insertion point of the subalar-coxal muscle (SA.Cm; Figs. 18, 19).

Muscles of the mesothorax

Dorsal muscles

MTm: The median tergal muscle (Fig. 14) is anteriorly attached to the first phragma and the anterior part of the scutum and runs to the posterior (or second) phragma. It is almost half the height of the mesothorax. The contraction of MTm results in downwards movement of the wings.

t13: The second dorsal longitudinal muscle (Figs. 14–17) is anteriorly attached to the scuto-scutellar impression and runs to the scutellum. It is a very small and flat muscle, lying posterior to MTm. It consists of only a few fibres.

S.LPNm: The scuto-lateropostnotal muscle (Figs. 15, 16) is attached to the posterior part of the scutum (PSp) and runs in almost vertical direction to the latero-ventral part of the phragma – the lateropostnotum (LPN). Ventrally the muscle is a little wider than dorsally. S.LPNm lies slightly lateral to MTm.

Dorso-ventral muscles

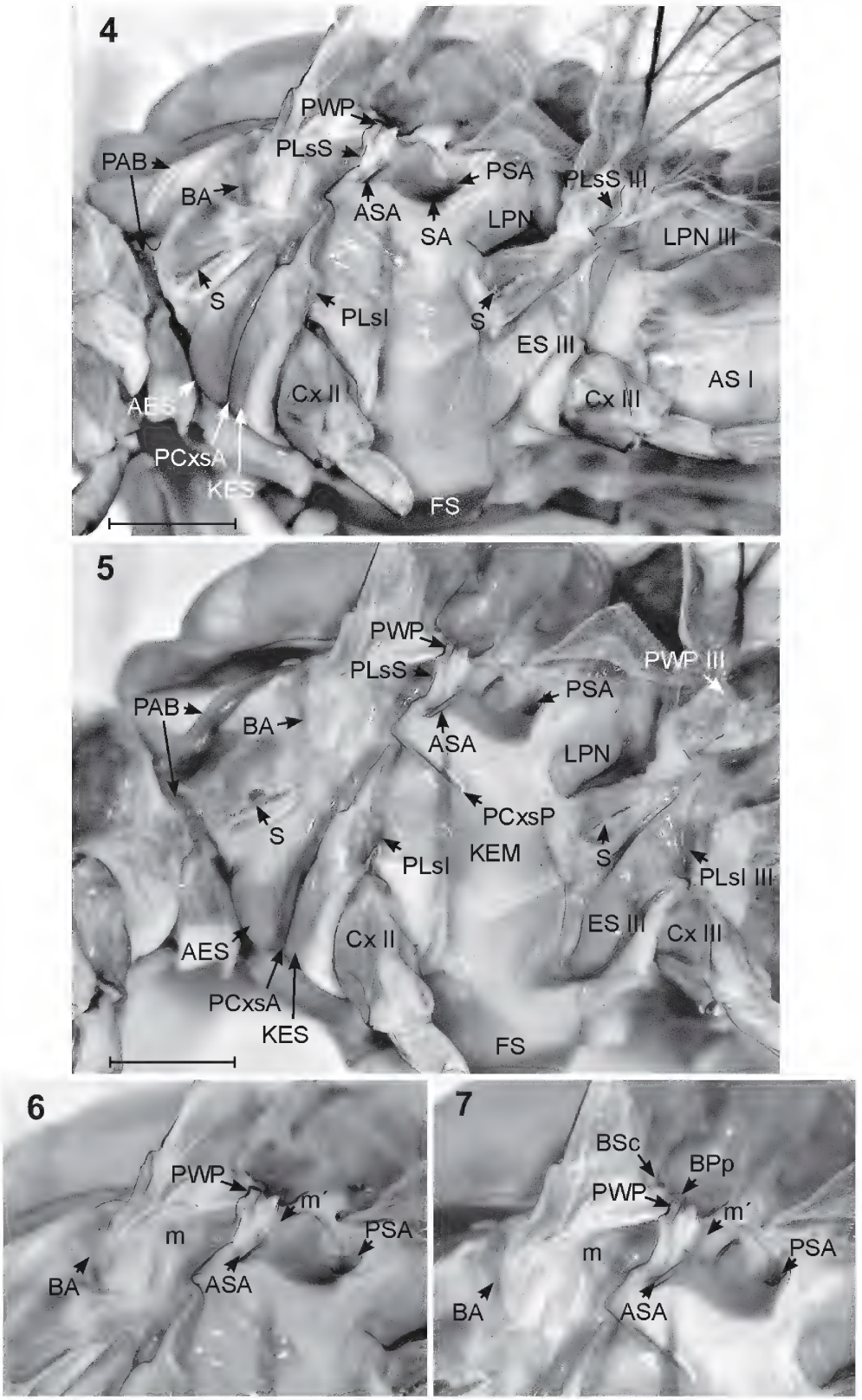
S.ESm: The scuto-episternal muscle (Fig. 15) is dorsally attached to the anterior part of the scutum and extends to the ventral part of the episternum. It is a large muscle lying lateral to MTm. It is dorsally wider than ventrally. The dorsal area of attachment is a little less than one third of the length of the mesothorax. S.ESm is the main antagonist to MTm.

S.CmA: The anterior scuto-coxal muscle (Figs. 15, 16) is dorsally attached to the lateroparapsidal suture and proceeds to the anterior rim of the coxa. It lies postero-lateral to the S.ESm.

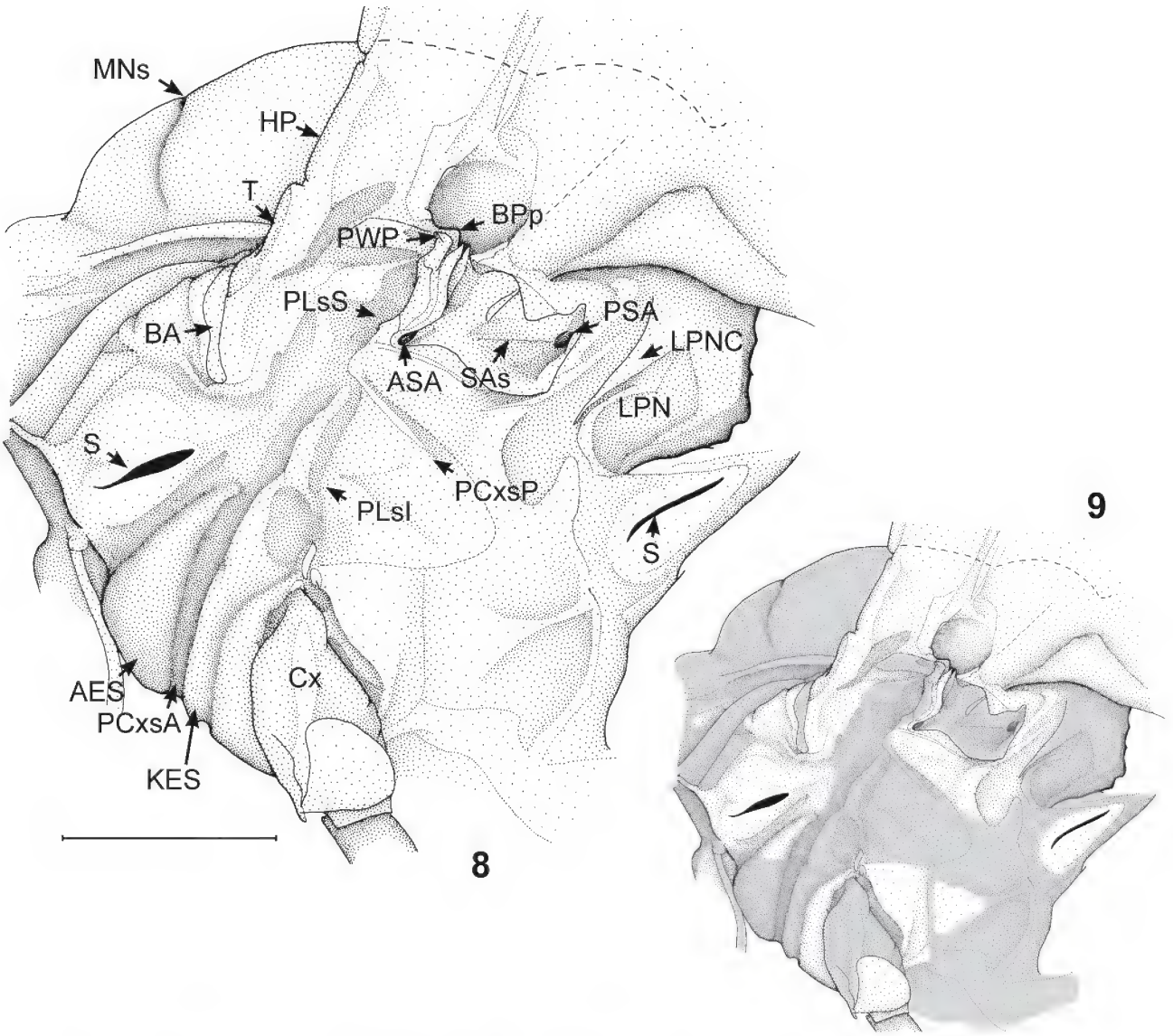
S.CmP: The posterior scuto-coxal muscle (Figs. 16, 17) runs from the posterior part of the scutum (anterior part of the posterior scutal protuberance, PSp) to the posterior rim of the coxa. S.CmP is located postero-lateral and in close proximity to S.CmA. This muscle is roughly similar in size as the S.CmA.

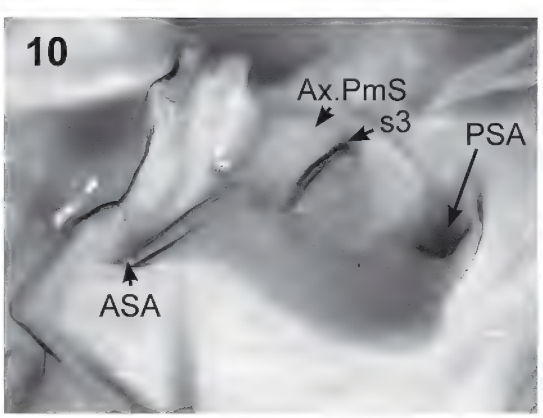
S.Trm: The scuto-trochanteral muscle (Figs. 17, 18) is dorsally attached to the sublateroscutum (SLS; Fig. 2) and proceeds to the trochanter. It is a flat muscle, which is thinner than the S.CmA and the S.CmP and lies lateral to the latter.

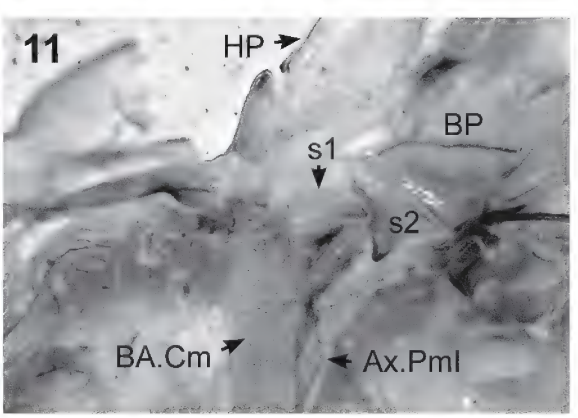
PSL.Cm: The parascutello-coxal muscle (Fig. 18) extends from the antero-lateral part of the scutellum, the parascutellum, to the postero-lateral rim of the coxa. The ventral point of attachment lies besides the ventral point of attachment of the subalar-coxal muscle. The PSL.Cm is a flat and slender muscle, which lies lateral



Figs. 4–7. *Siphlonurus aestivalis*, ♀ (4, 6) and ♂ (5, 7) imago. – **4–5**. Pleurum of meso- and metathorax. **6–7**. Mesopleurum, upper area. – m = ventral attachment of BA.Pm; m′ = ventral attachment of Ax.PmS. – Scales: 1 mm.







Figs. 8–11. *Siphlonurus aestivalis*, ♂ (8–10) and ♀ (11) imago. – **8–9**. Mesopleurum (grey areas sclerotised). **10**. SA of the mesopleurum (Ax.PmS and s3 shine through the SA). **11**. Mesothorax, internal view, dorsal attachment of BA.Cm and Ax.PmI. – Scale: 1 mm.

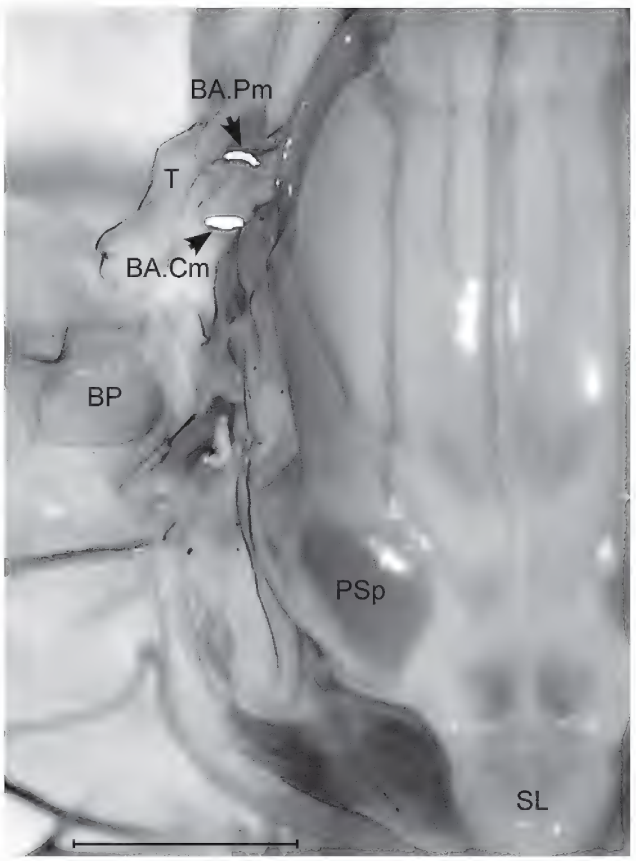


Fig. 12. *Siphlonurus aestivalis*, ♀ imago, left fore wing base and attachment points of BA.Pm and BA.Cm. – Scale: 1 mm.

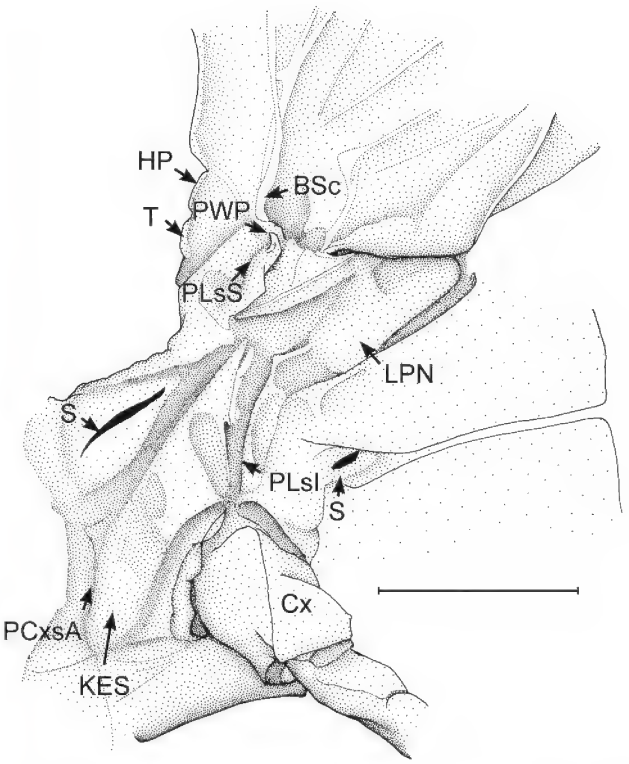


Fig. 13. *Siphlonurus aestivalis*, ♂ imago, metapleurum. – Scale: 1 mm.

to S.LPNm. The dorsal part of this muscle is slender but robust (wider than in most other Ephemeroptera) and is ventrally attached to the coxal rim via a long, probably epidermal tendon.

AN.Pm: The anteronoto-pleural muscle (Figs. 16, 17) is dorsally attached to the antero-lateral part of the scutum and extends to the dorsal part of the anterior paracoxal suture. It is a flat but distinct and relatively robust muscle (more distinct than in other Ephemeroptera, e. g. *Habroleptoides confusa*). AN.Pm lies anterior to SrA.Pm and medial to the basalar-sternal muscles (BA.SmS, BA.SmI).

SrA.Pm: The suralar-pleural muscle (Figs. 16–18) is dorsally attached to the suralare (SrA; Fig. 2), which includes the anterior notal wing process. Ventrally, it is attached to the paracoxal suture (below the posterior pleural suture). In some specimens the ventral point of attachment is somewhat antero-dorsal: In this case, the muscle is ventrally attached to the dorsal part of the AES. The SrA.Pm is a flat muscle consisting of only a few fibres.

Pleural muscles

P.Cm: The pleuro-coxal muscle (Figs. 17–19) runs from the anterior paracoxal suture to the anterior coxal rim. It is a short muscle, which is oval in cross section.

P.Trm: The pleuro-trochanteral muscle (Figs. 17–19) is dorsally attached to the anterior paracoxal suture and ventrally to the trochanter. It is a slender muscle lying direct posterior to P.Cm. P.Trm is almost round in cross section.

Ventral muscles

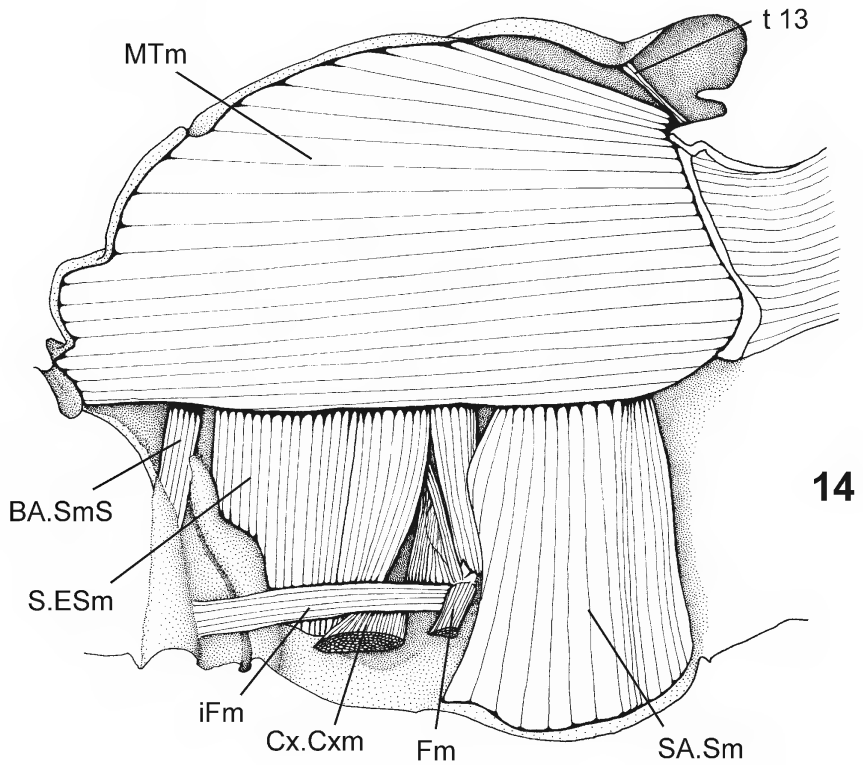
iFm: The intersegmental furcal muscle (Fig. 14) runs from the posterior side of the profurca to the anterior side of the mesofurca. It is a flat but distinct muscle.

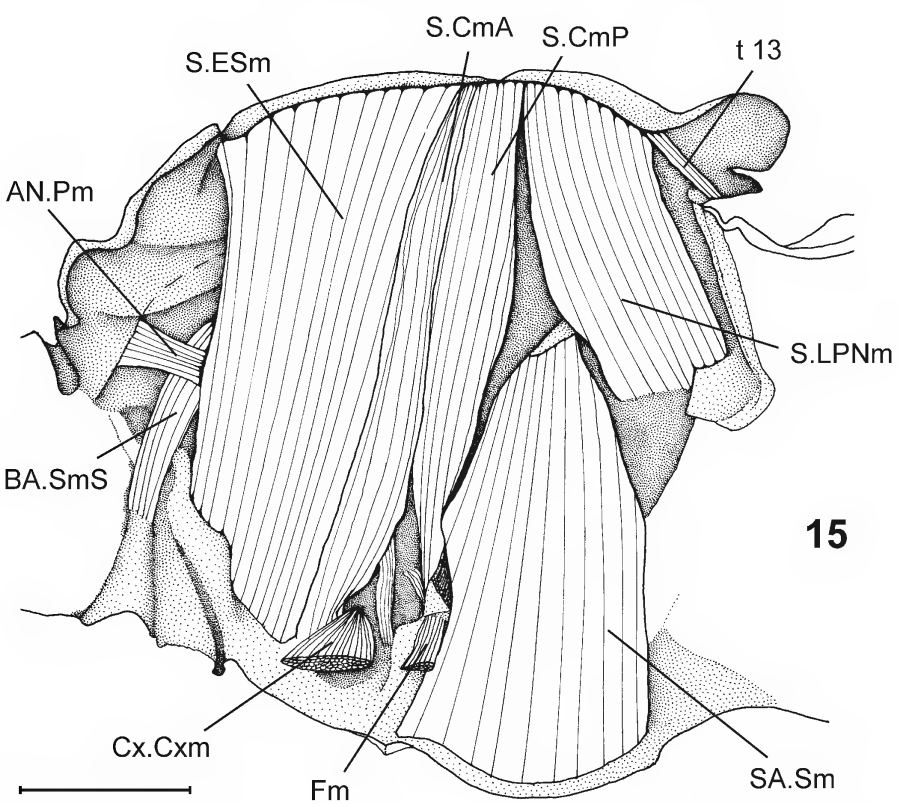
Fm: The furcal muscle (Figs. 14–16) runs from the medial side of the right sternal apophysis (right furca) to the medial side of the left sternal apophysis (left furca).

F.CmP: The posterior furco-coxal muscle (Figs. 18, 19) is a flat muscle running from the posterior side of the furca to the coxal rim (next to the coxo-pleural articulation and the ventral attachment of the BA.Cm).

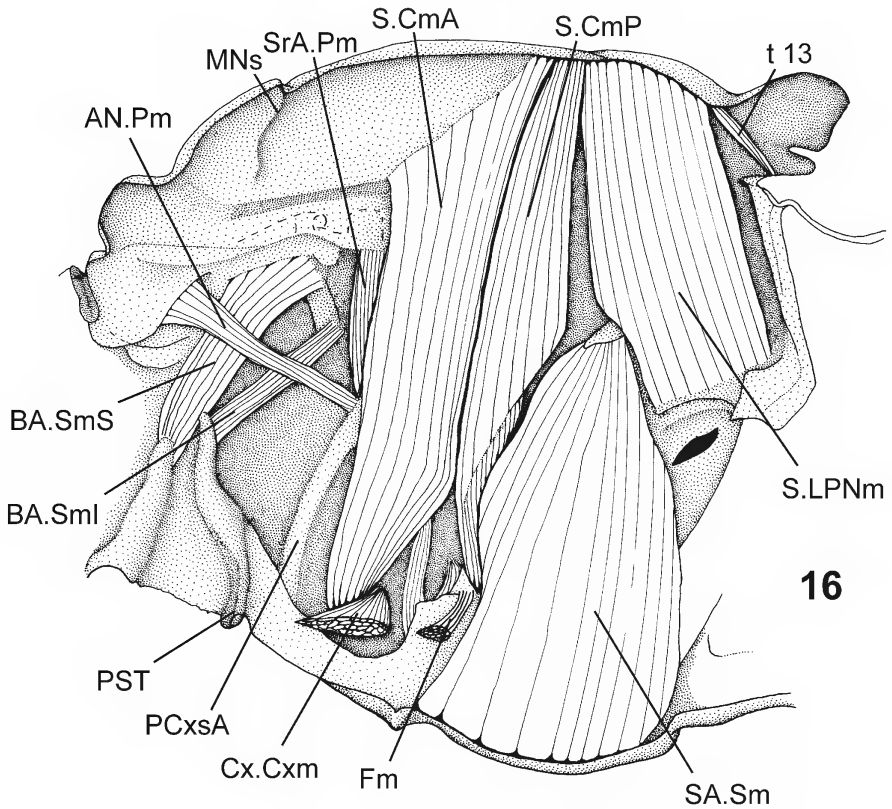
Direct flight muscles

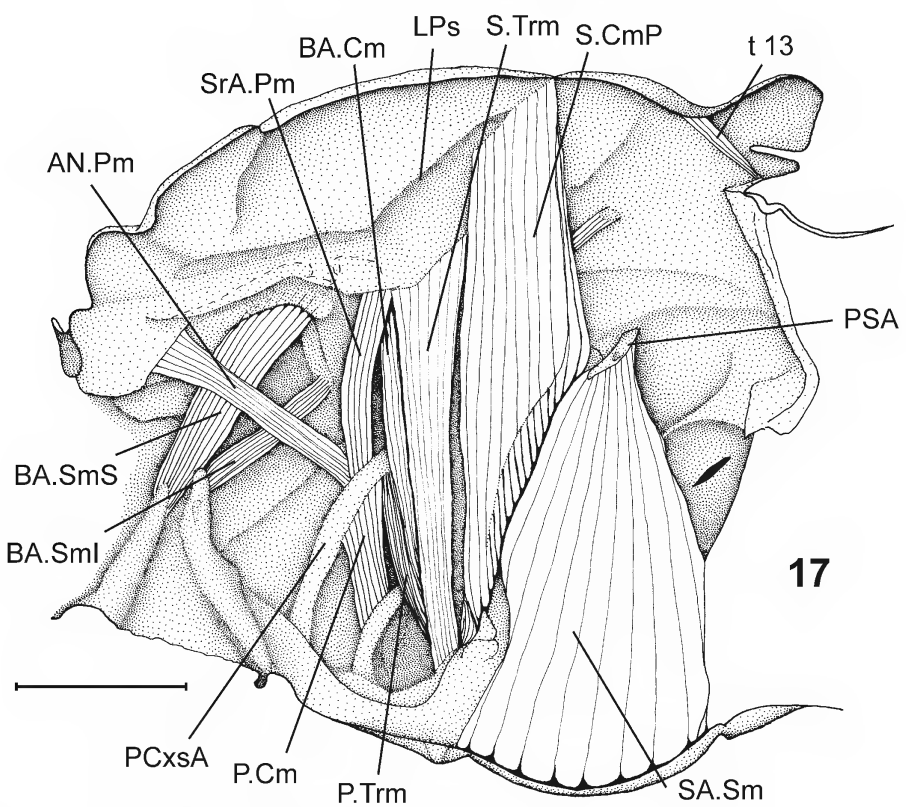
BA.SmS: The superior basalar-sternal muscle (Figs. 14–19) is dorsally attached to the crescent-shaped basalare



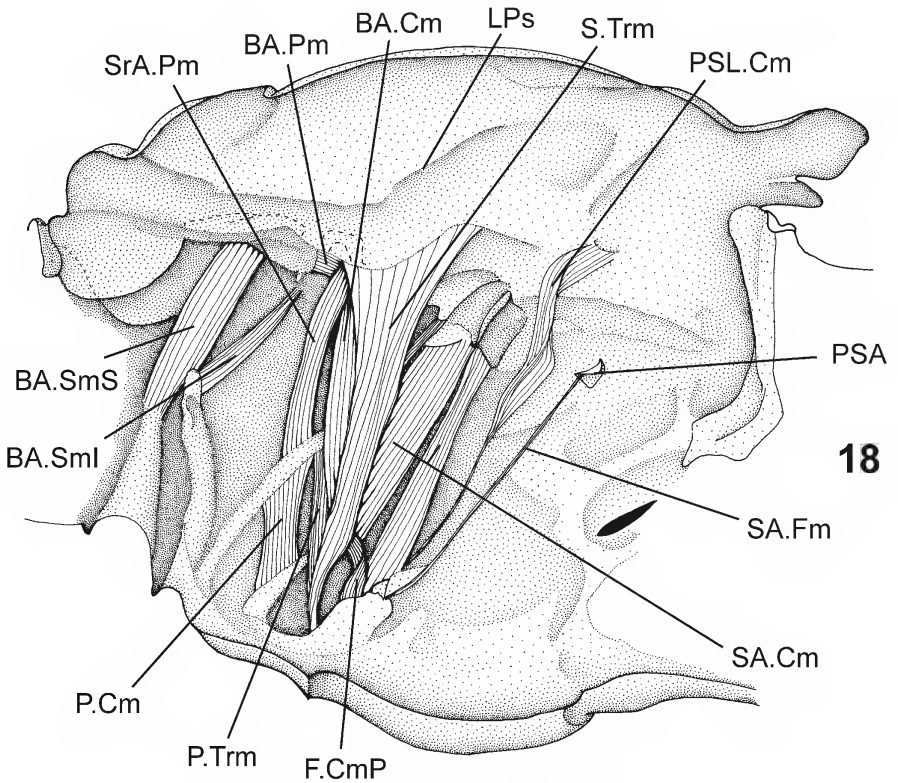


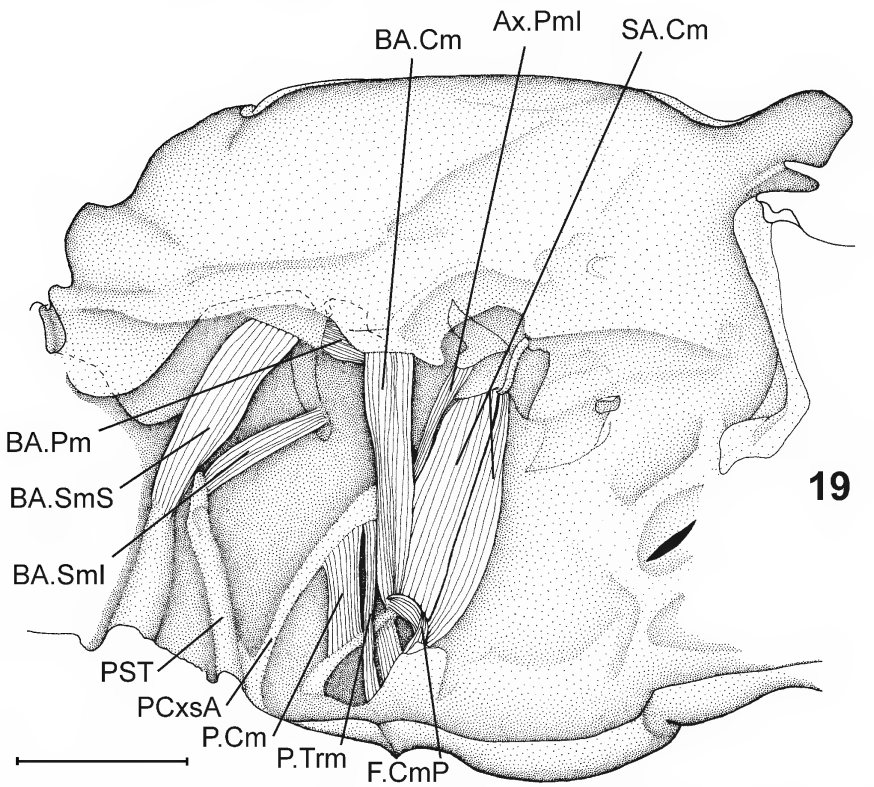
Figs. 14–15. *Siphlonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (14) and progressively proceeding to the most lateral muscles (see Fig. 19). – Scale: 1 mm.



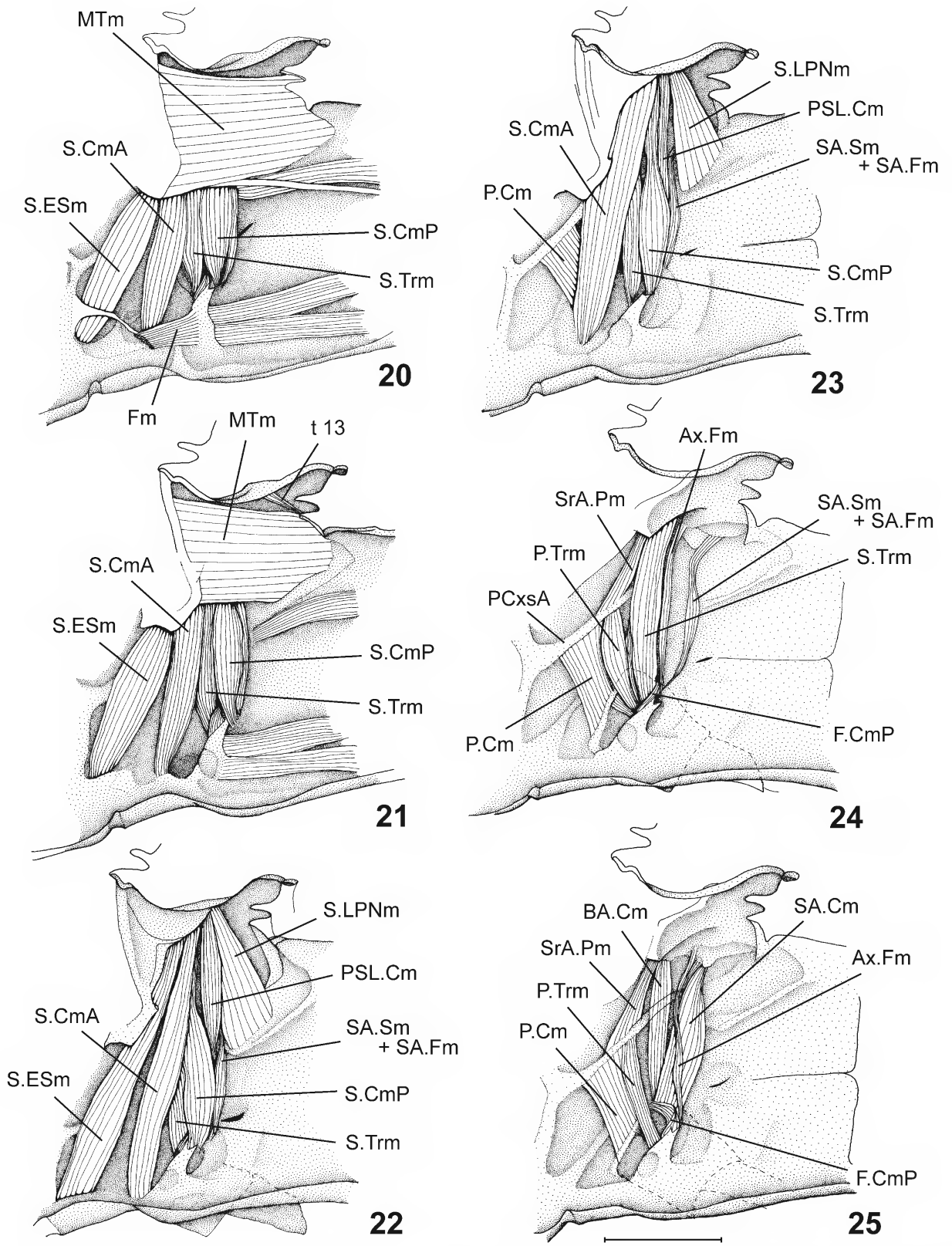


Figs. 16–17. *Siphlonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 14–15). – Scale: 1 mm.





Figs. 18–19. *Siphlonurus aestivalis*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 14–15). – Scale: 1 mm.



Figs. 20–25. *Siphlonurus aestivalis*, ♀ imago, musculature of the right half of the metathorax at progressive stages of dissection, starting with median muscles (20) and progressively proceeding to the most lateral muscles (Fig. 25). – Scale: 1 mm.

and runs to the profurca or directly posterior to it. The superior basalar-sternal muscle is considerably larger than the very small inferior one.

BA.SmI: The inferior basalar-sternal muscle (Figs. 16–19) runs from the ventral part of the crescent-shaped basalare to the presternite (PST, compare Fig. 48). It is much smaller than the BA.SmS (only about one quarter of its size).

BA.Pm: The basalar-pleural muscle (Figs. 18, 19) is a short but robust muscle running from a sclerite, lying in-between the tegula and the tergum, to the pleurum – anterior to the PWP.

BA.Cm: The basalar-coxal muscle (Figs. 17–19) is dorsally attached to a sclerite, lying antero-medial to s1. It proceeds to the coxal rim (adjacent to the coxo-pleural joint). BA.Cm is located antero-lateral to SrA.Pm.

SA.Sm: The subalar-sternal muscle (Figs. 14–17) is dorsally attached to the ventral part of the subalare and to the posterior subalar apodeme (PSA). It extends to the furcasternum. It is the largest subalar muscle, ventrally slightly wider than dorsally and located posterior to S.CmP.

SA.Fm: The subalar-furcal muscle (Fig. 18) is a very slender muscle running from the posterior subalar apodeme (PSA) to the furca. It is located anterior to SA.Sm.

SA.Cm: The subalar-coxal muscle (Figs. 18, 19) is dorsally attached to the anterior part of the subalare, i. e. the anterior subalar apodeme (ASA). The SA.Cm consists of two parts. The first part is more compact and runs to the latero-posterior part of the coxal rim (near the coxo-pleural joint). The second part, which lies lateral to the first part, is rather flat and runs to the posterior rim of the coxa. The insertion as well as the origin of the second part is wide. SA.Cm is located anterior to SA.Sm.

Ax.Fm: The axillar-furcal muscle (not pictured, compare Figs. 53, 119–122: t-s 3) is a very slender muscle running from the proximal apodeme of the second wing base sclerite (s2) to the tip of the furca.

Ax.PmI: The (inferior) axillar-pleural muscle (Fig. 19) runs from the ventral side of the proximal apodeme of the second wing base sclerite (s2) to the pleural ridge. Both the Ax.Fm and the Ax.PmI are slender but robust muscles that are distinct in the mesothorax.

Ax.PmS: The (superior) axillar-pleural muscle (not pictured, compare Figs. 54, 55) is a short but robust muscle running from the third wing base sclerite (s3) to the anterior part of the subalare.

Cx.Cxm: The coxo-coxal muscle (Figs. 14–16) is present. It stretches from the antero-lateral interior area of the right coxa to the antero-lateral interior area of the left coxa. The muscle is located anterior to the furco-furcal muscle (Fm) and is about two to three times as large as the Fm.

External morphology of the metanotum

The metanotum is rather flat. Its sutures are more or less reduced in comparison to the mesonotum. The scutum and the scutellum (SL) are short and approximately equal in length. The posterior scutal protuberances (PSp) are visible. Posterior to the PSp is the scutellum; its dorsal and lateral parts (scutellum, SL, and parascutellum, PSL) are distinct.

The median longitudinal suture (MLs) is indistinct and just visible at the anterior part of the scutum.

The elements of the metathoracic wing base are partially reduced. The anterior and the posterior notal wing processes (ANP, PNP) are distinct in the metanotum. The PNP articulates with the third free wing base sclerite (s3). The tegula is located at the anterior part of the wing base, between the tergum and the humeral plate (HP); it is discernible even in the hind wing. The humeral plate (HP) is located distal to the tegula; it is conspicuous in the metathorax but T and HP are rather membranous and soft.

The major part of the basal plate (BP) is clearly convex and distinct. Its proximal area is flat and clearly distinguishable from the convex area of the basal plate.

The first free (anterior) wing base sclerite (s1) is missing. The second free wing base sclerite (s2) is conspicuous and broad (roughly like the mesothoracic s2). It has a distinct proximal process, which is slightly bent inwards. The third free wing base sclerite (s3) is, like the second sclerite, discernible in the metathoracic wing base.

The basanale of the hind wing is hard to distinguish from s3. The costal brace (cb) at the anterior part of the wing is conspicuous. The anterior part of the anal brace (ab) is arched and rather indistinct. The proximal (or posterior) arc of the anal brace is conspicuous. The distal (or anterior) arc of the anal brace is rather indistinct. The distinct subcostal vein (Sc) originates at the antero-ventral part of the basal plate. The anterior radial vein originates at the antero-dorsal part of the basal plate. The base of the anterior medial vein (MA) is located directly posterior to the anterior radial vein and it is discernable almost to the basal plate.

The lateropostnotum (LPN) is developed as a distinct convex area (similar to the mesothorax).

External morphology of the metapleurum

The anterior paracoxal suture (PCxsA; Fig. 13) is the most conspicuous suture in the metapleurum. It divides the narrow anepisternum (AES) from the much wider katepisternum (KES; Fig. 13). The posterior paracoxal suture (PCxsP) is indistinct in the metapleurum. A further conspicuous suture is the pleural suture (PLsS, PLsI; Figs. 5, 13). It divides the wider episternum (ES; Figs. 4, 5) from the narrow epimeron. Dorsally the PLsS extends into the distinct pleural wing process (PWP; Fig. 13). The basal part of the subcostal vein (BSc; Fig. 13) is also distinct.

A basalare (BA) is not visible. The dorsal part of the subalare (SA, not pictured) is partly noticeable as a narrow sclerite, while the ventral part is inconspicuous.

Muscles of the metathorax

Dorsal muscles

MTm: The median tergal muscle (Figs. 20, 21) stretches between the two phragmata. It is a very large muscle in relation to the size of the metathorax.

t13: The second dorsal muscle (Fig. 21) runs from the notum (in-between the scutum and the scutellum, lateral to the MLs) to the dorsal part of the phragma between the metathorax and the abdomen. The muscle is small, flat and consists of only a few fibres, though it is approximately equal in size to t13 of the mesothorax.

S.LPNm: The scuto-lateropostnotal muscle (Figs. 22, 23) runs from the posterior part of the scutum to the small lateropostnotum. It is a relatively large muscle comparable in size to that of the mesothorax. The ventral point of attachment is wider than the dorsal one.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle (Figs. 20–23) runs from the antero-median part of the triangular scutum to the episternum. It is a large muscle in the metathorax.

S.CmA: The anterior scuto-coxal muscle (Figs. 20–23) is dorsally attached to the scutum – postero-lateral to the dorsal point of attachment of the S.ESm and runs to the anterior coxal rim. It is a large muscle, which is only slightly smaller than S.ESm.

S.CmP: The posterior scuto-coxal muscle (Figs. 20–23) runs from the scutum (posterior to the S.CmA) to the posterior coxal rim. The S.CmP is smaller and more slender than the S.CmA.

S.Trm: The scuto-trochanteral muscle (Figs. 20–24) is dorsally attached to the lateral part of the scutum (lateral to S.CmA and S.CmP, proximal to the BP of the wing base and at the same level). Ventrally, the muscle is attached to the antero-medial area of the trochanter. S.Trm is almost half the size of S.ESm.

PSL.Cm: The parascutello-coxal muscle (Figs. 22, 23) runs from the anterior part of the scutellum to the postero-lateral part of the coxal rim. The dorsal half of PSL.Cm is broad. The muscle is ventrally attached to the coxal rim via a tendon. It is a comparably large metathoracic muscle, which is as large if not larger than its mesothoracic equivalent.

AN.Pm: The anteronoto-pleural muscle (not pictured) is dorsally attached to the antero-lateral part of the notum and extends to the dorsal part of the anterior paracoxal suture just dorsally of the P.Trm. It is a flat and wide but distinct and relatively robust muscle.

SrA.Pm: The suralar-pleural muscle (Figs. 24, 25) is dorsally attached to the lateral part of the scutum and runs to the dorsal part of the anterior paracoxal suture. It is a very slender muscle consisting of only a few fibres.

Pleural muscles

P.Cm: The pleuro-coxal muscle (Figs. 23–25) is stretched between the anterior paracoxal suture (PCxsA) and the anterior rim of the coxa. The muscle seems to consist of two parts and it is rather flat but broad.

P.Trm: The pleuro-trochanteral muscle (Figs. 24, 25) runs from the PCxsA to the trochanter and is almost round in cross section.

Ventral muscles

Fm: The furcal muscle (Fig. 20) runs from the medial side of the right sternal apophysis (right furca) to the medial side of the left sternal apophysis (left furca). It is a flat muscle.

F.CmP: The flat posterior furco-coxal muscle (Figs. 24, 25) runs from the furca to the coxal rim, where the BA.Cm is attached to the coxo-pleural joint.

Direct flight muscles

BA.SmS: The superior basalar-sternal muscle (not pictured) is diminished. It is a short and flat muscle running from the anterior part of the wing base to the membrane just posterior and above the stigma.

BA.SmI: The inferior basalar-sternal muscle is absent in the metathorax.

BA.Cm: The basalar-coxal muscle (Fig. 25) is dorsally attached to a small sclerite in the membrane (just as in the fore wing) and is ventrally attached to the coxal rim (near the coxo-pleural joint). It is a large, robust and distinct muscle.

BA.Pm: The basalar-pleural muscle (not pictured) is dorsally attached to a distinct triangular sclerite (anterior to s2) and runs posteriorly to the pleurum, anterior to the pleural suture. It is a robust and short muscle.

SA.Cm, **SA.Sm**, **SA.Fm**: The subalare is small in the metathorax and its apodemes are inconspicuous externally. Furthermore, the anterior basisternum and the posterior furcasternum are inconspicuous and the first abdominal sternite is located shortly posterior to the metacoxa. The subalar muscles are small and not as conspicuous as in the mesothorax. Two muscles are distinguishable: The first one (SA.Cm; Fig. 25) is dorsally attached to the anterior section of the subalare and is ventrally attached to the coxal rim. It is a flat but relatively broad muscle. Posterior to the SA.Cm is the dorsal point of attachment of the second, slender part (SA.Sm, SA.Fm; Figs. 23, 24). It is ventrally attached

to the posterior rim of the coxa and a few fibres are attached to the tip of the furca.

Ax.Fm: The axillar-furcal muscle (Figs. 24, 25) is a very slender muscle running from the process of the s2 to the tip of the furca. It is almost as large as the Ax.Fm of the mesothorax.

Ax.PmI: The inferior axillar-pleural muscle (not pictured) is dorsally attached to the process of s2 (anterior to the Ax.Fm) and runs to the pleural suture. It is a slender muscle consisting of only a few fibres.

Ax.PmS: The superior axillar-pleural muscle (not pictured) is a short but robust muscle running from s3 to the pleurum (posterior to the PWP).

Cx.Cxm: The coxo-coxal muscle (not pictured) is present in the metathorax and runs from the anterior rim of the left coxa to the anterior rim of the right coxa.

3.2.3 *Baetis* sp., winged stages (Figs. 26–37) (n = 13)

Measurements (of the described ♀ specimen)
Total length: 6.25 mm. – Length of mesothorax: 1.5 mm. – Length of metathorax: 0.65 mm. – Height of mesothorax: 1.5 mm (0.9 mm belong to MTm). – Height of metathorax: 1 mm.

External morphology of the mesonotum

The anteronotal protuberance (ANp; Fig. 26) and the impression (ANi; Fig. 26) posterior to it are distinct. Anterior to the scutellum are the prominent paired posterior scutal protuberances (PSp; Fig. 26), which are approximately in the centre of the scutum. The PSp are longish rather than circular. The scutellum (SL; Fig. 26) and its lateral parts are distinct.

The median longitudinal suture (MLs; Fig. 26) is conspicuous in the centre part of the scutum. It disappears anteriorly next to the ANi and ANp and posteriorly next to the SL. The medioparapsidal sutures (MPs; Fig. 26) are at least as distinct as the MLs and converge posteriorly. Lateral to the MPs run the distinct lateroparapsidal sutures (LPs; Figs. 26–29), which are also posteriorly convergent. The conspicuous antero-lateral scutal costa (ALSC; Fig. 26) is located at the antero-lateral part of the scutum. The mesonotal suture (MNs) is not visible.

The anterior and the posterior notal wing processes (ANP, PNP; Figs. 27–29) of the wing base are distinct. Nevertheless, the ANP is rather short while the PNP is conspicuous. The tegula (T; Figs. 27, 29, 33) at the anterior wing base is densely covered with short setae in subimagines, whereas in adults there are distinctly less setae.

At the anterior base of the wing, a two armed sclerite is visible, which is connected to the crescent-shaped sclerite (BA; Figs. 30–33). The anterior branch lies medial to the tegula and the posterior branch lies anterior to the first free wing base sclerite (s1; Figs. 27–29). The basalar-pleural muscle (BA.Pm, not pictured) is attached to the anterior part of the sclerite, while the basalar-coxal muscle (BA.Cm, not pictured) attaches to the posterior part of the sclerite.

The basal plate (BP; Figs. 27–29) of the wing base is convex, but in several specimens this was not as distinct as in other Ephemeroptera. The proximal base of the basal plate is clearly demarcated and has a process anteriorly and also a conspicuous process posteriorly. The proximal process is the dorsal attachment point of the axillar-furcal muscle (Ax.Fm, not pictured). The first free wing base sclerite (s1; Figs. 27–29) is a rather large triangular sclerite, which is sclerotised only in the dorsal layer of the wing membrane. It articulates with the ANP proximally. No muscle is attached to it. The second free wing base sclerite (s2, not pictured) seems to be diminished in size. The third free wing base sclerite (s3; Figs. 27–29) articulates with the basal plate anteriorly and with the PNP posteriorly. A muscle is attached to the proximal part of this conspicuous sclerite, and this muscle runs to the pleurum posterior to the PWP. The distinct basanale (ban; Fig. 29) posterior to the s3 is sclerotised.

Most of the wing veins disappear at the wing base. However, the costal vein, the subcostal vein and the anterior radial vein are conspicuous even at their bases. The radial sector and the anterior medial vein converge at their bases but are not distinctly connected. The sector of the medial veins disappears at the base. The anterior cubital vein and the anterior anal vein are discernable next to the anal brace. Both the anal and the costal brace are conspicuous.

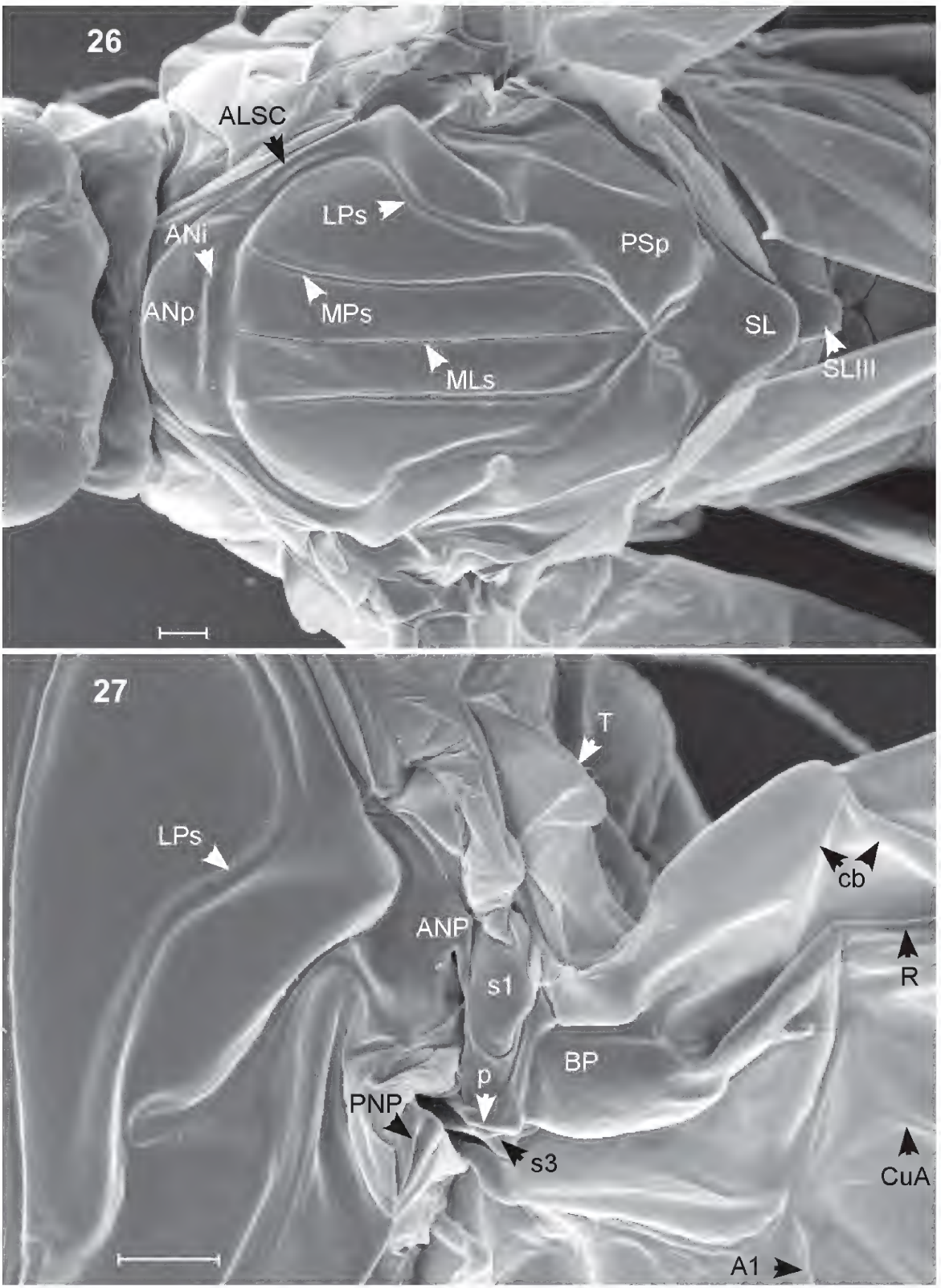
The lateropostnotum (LPN; Fig. 32) is rather small and triangular in shape in the examined specimens.

External morphology of the mesopleurum

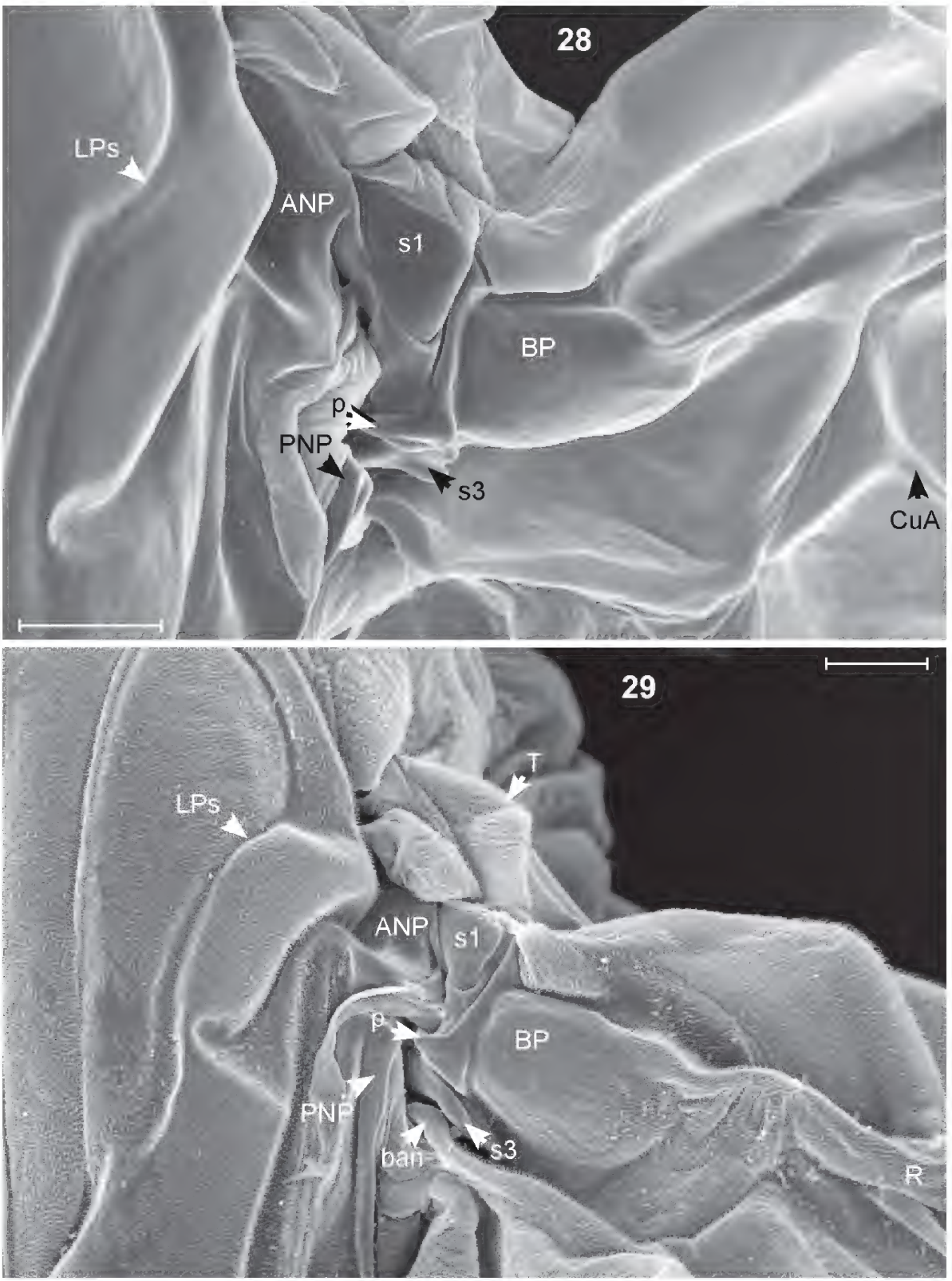
The three branches of the prealar arms are rather long. The dorsal and the ventral arc are connected to each other and the posterior arc reaches the anterior wing base at the same level as the tegula but medial to it. The spiracle lies in a large membranous area posterior to the prealar bridge.

The distinct anterior paracoxal suture (PCxsA; Fig. 32) separates the anepisternum (AES; Fig. 32) from the much broader katepisternum (KES; Fig. 32). The posterior part of the paracoxal suture (PCxsP; Fig. 32) is conspicuous in the mesothorax. It subdivides the upper anepimeron (AEM) from the lower katepimeron (KEM). Both AEM and KEM are narrow, though in several specimens the AEM is slightly broader than the KEM.

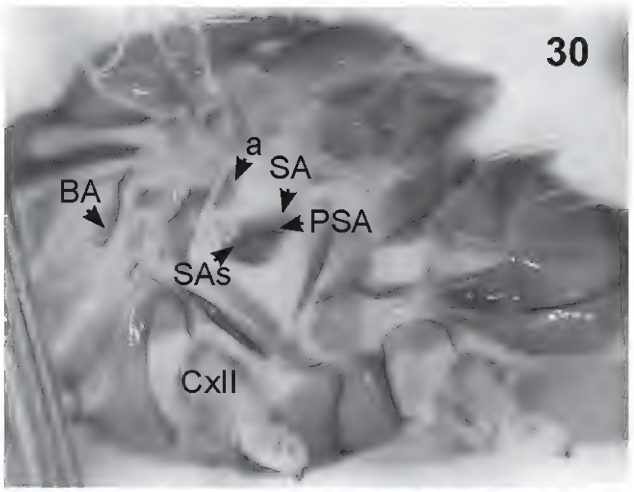
The upper part of the pleural suture (PLsS; Fig. 32) is distinct and runs obliquely forward. The pleural wing process (PWP; Figs. 32, 33) at the upper end of the pleural suture is small but clearly visible. The externally visible

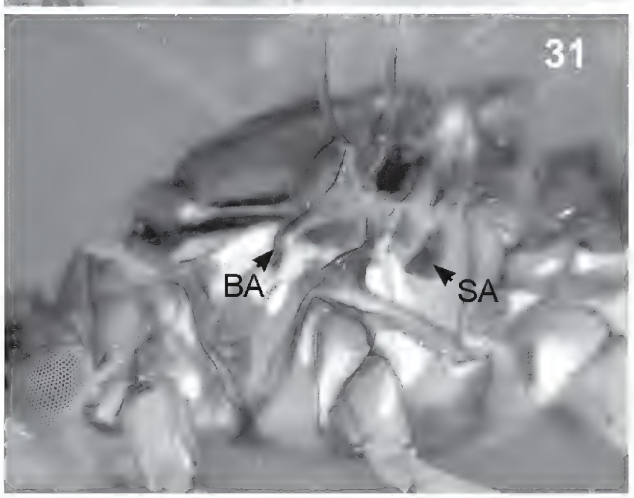


Figs. 26–27. *Baetis* sp. (SEM images), ♀ imago. – **26**. Mesothorax, dorsal view (head to the left). **27**. Base of right fore wing. – SL III = scutellum of the metathorax; p = posterior proximal process of the basal plate. – Scales: 0.1 mm.

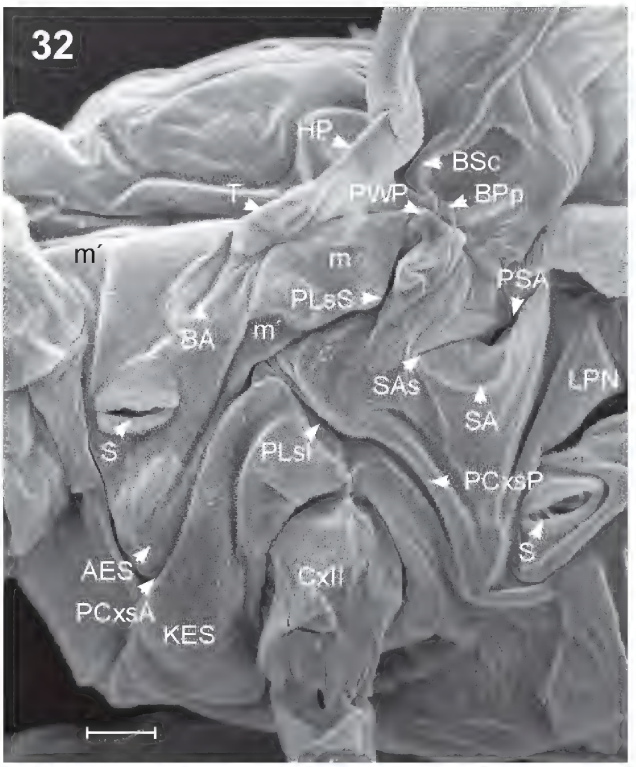


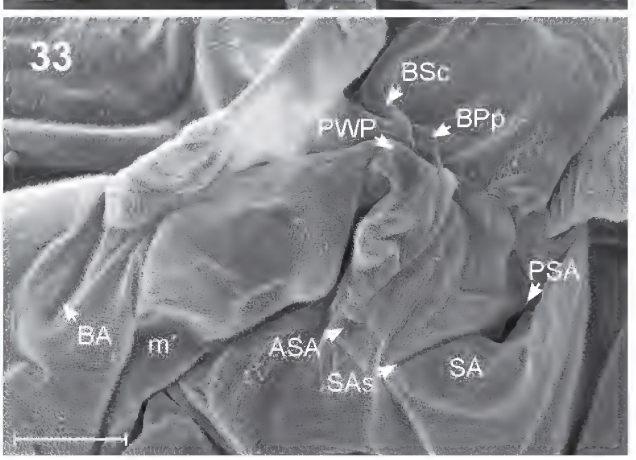
Figs. 28–29. *Baetis* sp. (SEM images), detail of the right fore wing base. – **28**. ♀ imago. **29** ♀ subimago. – p = posterior proximal process of the basal plate. – Scales: 0.1 mm.





Figs. 30–31. *Baetis* sp., overview of the mesopleurum of *Baetis* sp. – **30**. ♂ imago. **31**. ♀ imago.





Figs. 32–33. *Baetis* sp. (SEM images), ♀ subimago. – **32**. Mesopleurum **33**. Mesopleurum, detail of upper area. – m = ventral attachment of BA.Pm; m´ = attachment points of AN.Pm. – Scales: 0.1 mm.

condylus of the PWP articulates with a ventral process of the basal plate (BPp; Figs. 32, 33) of the wing base. In some subimaginal specimens the upper part of the pleural suture is not as distinct as its lower part, i. e. the inferior pleural suture (PLsI; Fig. 32). The PLsI is conspicuous and runs obliquely towards the back (downwards) to the point where the coxa articulates with the pleurum.

Anterior to the PWP lies the basalare (BA; Figs. 30–33), which is curved slightly forwards. The subalare (SA; Figs. 31, 33) is located posterior to the PWP. The ventral part of the subalare is narrow but clearly visible sclerotised, whereas the dorsal part is rather inconspicuous in most of the examined specimens. Only the most anterior part of the SA, next to the PWP, is clearly sclerotised; it is a distinct and narrow sclerite. The subalar suture (SAs; Figs. 30, 32, 33), at the anterior rim of the posterior part of the subalare and the posterior apodeme (PSA; Figs. 30, 32, 33) are conspicuously developed. The anterior subalar apodeme (ASA; Fig. 33) is rather inconspicuous and usually not visible from outside.

Muscles of the mesothorax

Dorsal muscles

MTm: The median tergal muscle (Figs. 35–37) runs from the anterior to the middle phragma. It is a large muscle, which encompasses at least one half of the height of the mesothorax.

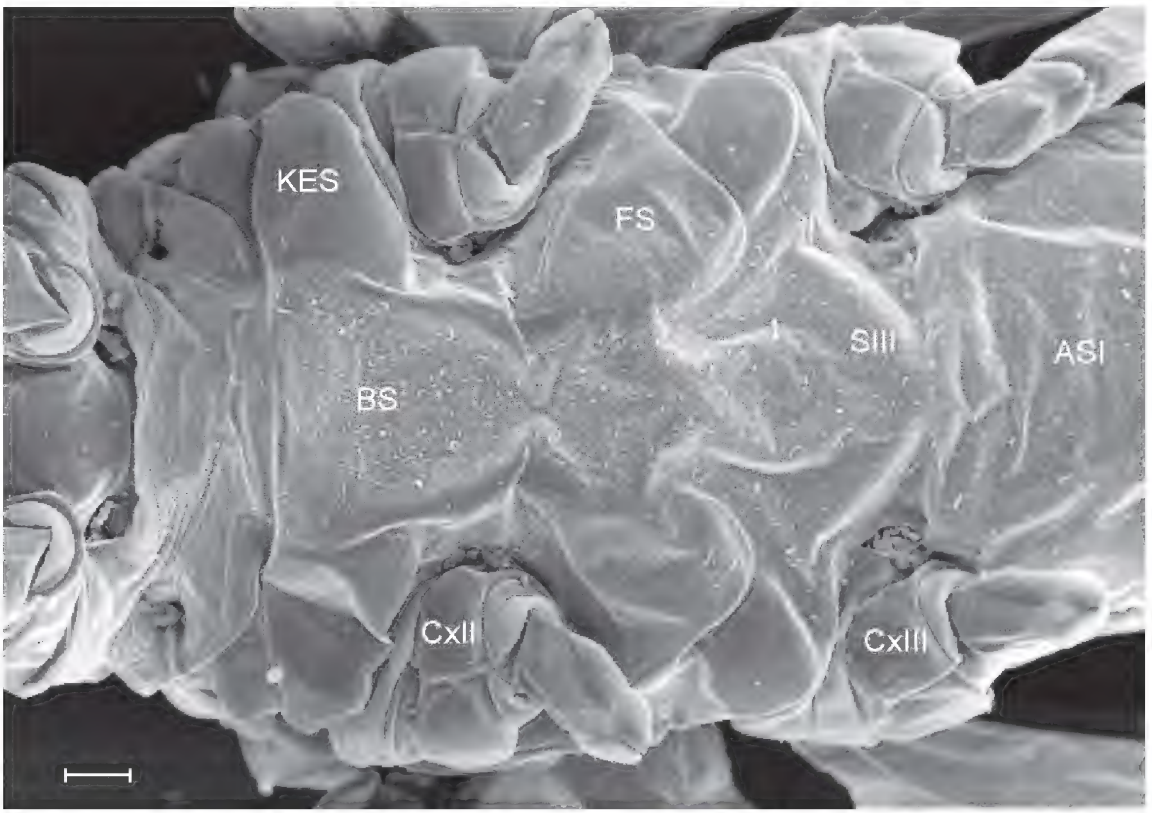


Fig. 34. *Baetis* sp. (SEM image), ♀ imago, mesosternum and metasternum, ventral view (head to the left). – Scale: 0.1 mm.

t13: It is absent in the mesothorax.

S.LPNm: The scuto-lateropostnotal muscle (Fig. 37) is dorsally attached to the posterior part of the scutum (PSp). Ventrally, it is attached to the lateropostnotum (LPN). It is a relatively large muscle, which is dorsally almost as wide as ventrally.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle (Figs. 35, 36) is dorsally attached to the scutum (just posterior to the ANi up to the part just anterior to the PSp and lateral to the MPs) and runs to the episternum. The ventral attachment encompasses only about one third of the area of the dorsal attachment. The area of the dorsal attachment encompasses approximately one half of the length of the mesothorax.

S.CmA: The anterior scuto-coxal muscle (not pictured) runs from the scutum, lateral to the lateroparapsidal sutures (LPs) to the anterior rim of the coxa. It is a flat muscle, which is not as wide as the S.ESm.

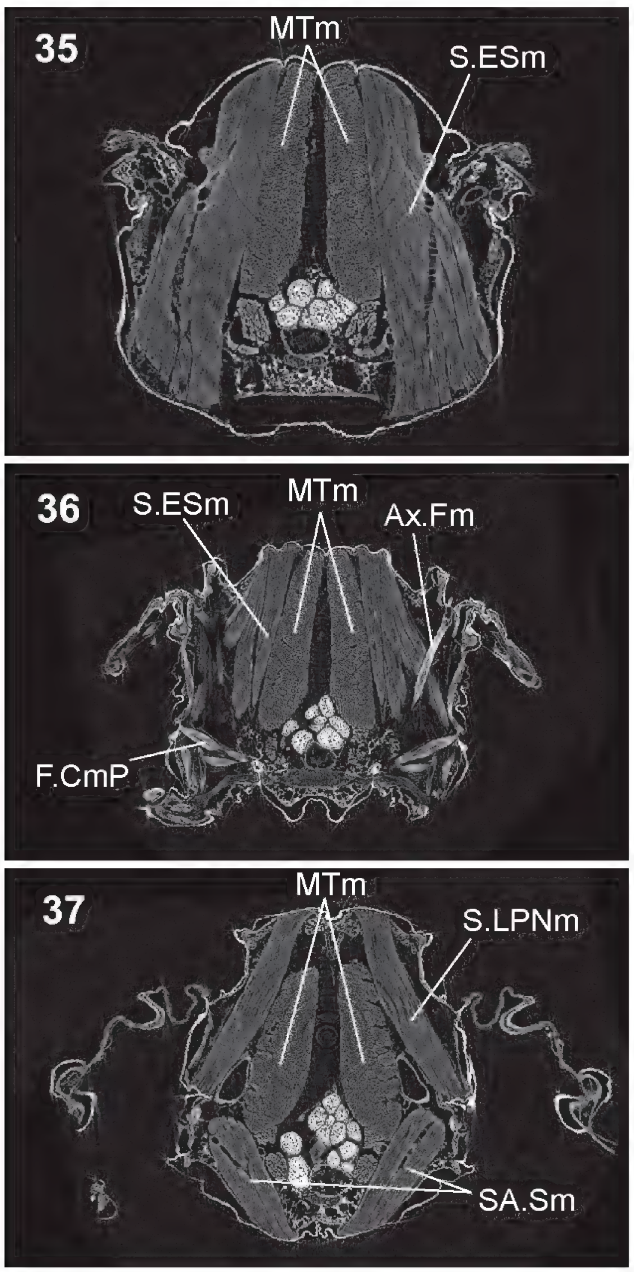
S.CmP: The posterior scuto-coxal muscle (not pictured) is dorsally attached to the scutum (just anterior to the S.LPNm and lateral to the S.CmA) and runs to the posterior coxal rim. The S.CmP is not as large as the S.CmA, approximately half as large as the S.ESm.

S.Trm: The scuto-trochanteral muscle (not pictured) runs from the lateral part of the scutum to the trochanter. It is a rather slender muscle, which is smaller than S.CmA and S.ESm.

PSL.Cm: The parascutello-coxal muscle (not pictured) is dorsally attached to the anterior area of the parascutellum and runs to the posterior rim of the coxa. The PSL.Cm is approximately as large as in other Ephemeroptera (if not slightly larger).

AN.Pm: The anteronoto-pleural muscle runs from the posterior arc of the prealar bridge (anterior part) to the anterior paracoxal suture (PCxsA, directly above the P.Cm) (Figs. 32, 33). It is a slender muscle consisting only of a few fibres.

SrA.Pm: The suralar-pleural muscle (not pictured) is dorsally attached to the anterior area of the suralare and ventrally attached to the anterior paracoxal suture (PCxsA, where the pleural suture and the posterior paracoxal suture are approximated) next to the AN.Pm. It is a flat but distinct muscle.



Figs. 35–37. *Baetis* sp., ♀ subimago, mesothorax (µCT-data), cross sections from anterior (35) to posterior (37).

Pleural muscles

P.Cm: The pleuro-coxal muscle (not pictured) runs from the anterior paracoxal suture (PCxsA) to the antero-lateral rim of the coxa. It is a flat but wide muscle.

P.Trm: The pleuro-trochanteral muscle (not pictured) is dorsally attached to the pleural suture and runs to the trochanter. It is a flat muscle, which is a little wider dorsally than ventrally.

Ventral muscles

iFm: The intersegmental furcal muscle (not pictured) is a slender muscle, running from the anterior part of the mesofurca to the presternite.

Fm: The furcal muscle (not pictured) is stretched between the left mesofurca and the right mesofurca. It is a short but robust muscle, which is almost elliptical in cross section.

F.CmP: The posterior furco-coxal muscle (F.CmP in Fig. 36) runs from the postero-lateral part of the furca to the coxo-pleural articulation point (just medial to the BA.Cm). It is a small and flat muscle.

Direct flight muscles

BA.SmS: The superior basalar-sternal muscle (not pictured) is dorsally attached to the upper part of the basalare (BA) and runs to the prothoracic furca.

BA.SmI: The inferior basalar-sternal muscle (not pictured) runs from the lower part of the basalare (BA) to the presternite. Both basalar-sternal muscles are slender and rather indistinct.

BA.Pm: The basalar-pleural muscle (Fig. 32) is dorsally attached to the sclerite, which is connected to the crescent-shaped sclerite (just posterior to the posterior arc of the prealar bridge). BA.Pm proceeds to the pleurum.

BA.Cm: The basalar-coxal muscle (not pictured) is dorsally attached to the posterior branch of the dorsal sclerite, just anterior to the first free wing base sclerite, and runs to the pleurum where the coxa articulates with the pleura. It is a slender muscle.

SA.Sm: The subalar-sternal muscle (Fig. 37) is dorsally attached to the posterior subalar apodeme (PSA) and ventrally attached to the furcasternite (FS; Fig. 34). The SA.Sm is slightly wider ventrally than dorsally.

SA.Fm: The subalar-furcal muscle runs from the PSA to the postero-lateral part of the mesofurca (sometimes it is shifted slightly medial to the medio-posterior rim of the coxa). It is a slender muscle, which is almost indistinguishable from SA.Sm.

SA.Cm: The subalar-coxal muscle (not pictured) is attached to the anterior subalar apodeme (ASA) and runs to the posterior part of the coxo-pleural articulation (just posterior to the BA.Cm). The anterior apodeme is reduced to a sclerotised and pigmented "bulge" and the SA.Cm is a much more slender muscle in the mesothorax of *Baetis* sp. compared to SA.Cm of other taxa.

Ax.Fm: The axillar-furcal muscle (Fig. 36) is attached to the proximal process at the postero-dorsal part of the basal plate (p in Figs. 27–29). It is a slender but distinct muscle in the mesothorax.

Ax.PmI: The inferior axillar-pleural muscle is not present.

Ax.PmS: The superior axillar-pleural muscle (not pic-

tured) is short but robust and stretches between the third free wing base sclerite (s3) and the pleurum.

External morphology of the metanotum

The hind wings in Baetidae are very small and the venation is reduced. In some genera the hind wings are even absent. The notum of the metathorax is also shortened.

The scutum is very short and the following scutellum is approximately as large as the scutum. The posterior phragma is extended posteriorly and visible from dorsal. The median longitudinal suture is visible from the middle of the scutum but most of the other sutures and convexities are indistinct in the metatergum. The wing base elements of the hind wings are reduced and partially missing.

External morphology of the metapleurum

Most of the sutures and sclerites that are distinct in the mesothorax are partly or completely reduced in the metathorax of *Baetis*. The upper part of the pleurum is rather less sclerotised, while the lower part is well sclerotised.

The inferior part of the pleural suture (PLsI) is conspicuous and runs obliquely towards the back (dorsoventrally). At its ventral end lies the coxo-pleural articulation. The superior part of the pleural suture (PLsS) is rather inconspicuous. The pleural wing process (PWP) at the upper point of the superior part of the pleural suture is small but distinct in the metapleurum. There is a small sclerite containing the PWP. Both the basalare, anterior to the PWP, and the subalare posterior to the PWP, are absent.

The anterior paracoxal suture (PCxsA) is partially conspicuous but the anepisternum (AES) and the katepisternum (KES) are hardly distinguishable.

Muscles of the metathorax

Dorsal muscles

MTm: The median tergal muscle is large and encompasses at least one half of the metathorax. It is anteriorly attached to the middle phragma and runs to the posterior phragma.

t13: The small dorsal muscle is not present in the metanotum.

S.LPNm: The scuto-lateropostnotal muscle is not present in the metathorax.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle is dorsally attached to the antero-lateral part of the scutum and runs to the episternum. It is the second largest muscle in the metathorax.

S.CmA: The anterior scuto-coxal muscle is dorsally attached to the antero-lateral part of the notum and proceeds to the anterior rim of the coxa. It is a flat muscle.

S.CmP: The posterior scuto-coxal muscle stretches from the medio-lateral part of the notum to the posterior part of the coxal rim. It is, like the S.CmA, a slender muscle.

S.Trm: The scuto-trochanteral muscle runs from the anterior part of the notum (just posterior to the S.CmA) to the lateral part of the trochanter. Compared to S.CmA and S.CmP it is a large muscle, almost twice as large as S.CmP.

PSL.Cm: The flat muscle running from the antero-lateral part of the scutellum to the postero-medial rim of the coxa is most likely the parascutello-coxal muscle.

AN.Pm: The anteronoto-pleural muscle is not present in the metathorax.

SrA.Pm: The suralar-pleural muscle is a flat muscle running from the antero-lateral part of the notum to the anterior paracoxal suture (PCxsA). It consists only of a few fibres.

Pleural muscles

P.Cm: The pleuro-coxal muscle runs from the anterior paracoxal suture (PCxsA) to the anterior rim of the coxa. It is a flat, but broad and robust muscle.

P.Trm: The pleuro-trochanteral muscle is dorsally attached to the anterior paracoxal suture (posterior to the P.Cm). Ventrally, it is attached to the trochanter. This slender but robust muscle is ventrally wider than dorsally.

Ventral muscles

iFm: The intersegmental furcal muscle is not present in the metathorax.

Fm: The furcal muscle runs from the left furca to the right furca. It is a robust muscle, of similar size as in the mesothorax.

F.CmP: The posterior furco-coxal muscle is attached to the furca and runs to the coxal rim next to the coxopleural joint. It is a robust muscle, which is distinct and about as large as the F.CmP of the mesothorax.

Direct flight muscles

Since the hind wings are only small, the direct flight musculature is also reduced in the metathorax.

BA.SmS, **BA.SmI**, **BA.Cm**, **BA.Pm**: The basalar muscles (superior basalar-sternal muscle [BA.SmS] as well as the inferior basalar-sternal muscle [BA.SmI], the basalar-pleural muscle [BA.Pm] and the basalar-coxal muscle [BA.Cm]) were not found in the metathorax.

SA.Cm, **SA.Sm, SA.Fm**: There is only one flat and small muscle in the postero-dorsal area of the pleurum. It is most likely the subalar-coxal muscle (SA.Cm), which attaches to the postero-lateral rim of the coxa. The subalar-sternal muscle (SA.Sm) and the subalar-furcal

muscle (SA.Fm) are most likely reduced in the metathorax.

Ax.Fm: The axillar-furcal muscle runs from the membrane at the wing base to the furca. It is a slender muscle, of similar size as the corresponding muscle in the mesothorax.

Ax.PmI/Ax.PmS: The inferior and the superior axillar-pleural muscles are not present.

3.2.4 *Ephoron virgo*, winged stages (Figs. 38–55) (n = 9)

Measurements (of the described ♂ specimen)

Total length: 11.5 mm. – Length of mesothorax: 2.8 mm. – Length of mesothoracic wing: 17.6 mm. – Width of mesothoracic wing: 8.2 mm. – Length of metathorax: 1.3 mm. – Length of metathoracic wing: 7.3 mm. – Width of metathoracic wing (measured at the tornus): 3.7 mm. – Height of mesothorax: 2.5 mm (1.4 mm belong to MTm). – Height of metathorax: 1.8 mm (0.66 mm belong to MTm).

External morphology of the mesonotum

The scutum is characteristic in *Ephoron virgo* since it is flat and its anterior part (ANp; Figs. 38, 39) relatively large, whereas the posterior part is rather short. The ANp is rather flat in specimens of *E. virgo* and its major part it is covered by the pronotum. The anterior notal impression (ANi; Fig. 38) is less distinct than in other mayflies (e. g. *Siphlonurus aestivalis*, *Habroleptoides confusa*). The posterior scutal protuberances (PSp; Figs. 38, 39, 41) are relatively large and conspicuous but also rather flat. Posterior to the PSp lies the scutellum (SL; Figs. 38, 39). The dorsal part of SL is long and narrow.

The sutures of the mesothorax are rather indistinct. The median longitudinal suture (MLs; Figs. 38, 42) is visible in the area from approximately the anterior notal impression (ANi) to the scutellum. At the anterior part of the scutum it is almost indistinguishable. The medioparapsidal sutures (MPs; Figs. 41–42) are rather faint and hardly visible in the mesotergum. The MPs are convergent posteriorly and join the lateroparapsidal sutures (LPs; Figs. 38, 39, 41, 42). The LPs, located lateral to the MPs, are not as distinct as in other mayflies. The antero-lateral scutal costa (ALSC) and the LPs are rather inconspicuous. The mesonotal suture (MNs) extends backwards and is also rather inconspicuous.

The anterior and posterior notal wing processes (ANP, PNP; Figs. 41, 42) are clearly distinguishable. The ANP is long and narrow and articulates with the first free wing base sclerite (s1; Fig. 41). The PNP is connected to the third free wing base sclerite (s3; Figs. 41, 42).

The tegula (T; Fig. 42) at the anterior base of the wing is not visibly covered with setae. Distal to the tegula lies the humeral plate (HP; Fig. 41). Between the wing base and the tergum are two separate sclerites visible.

The prominent basal plate (BP; Figs. 41, 42) is sclerotised in both dorsal and ventral layer of the wing membrane. The base of the subcostal vein (BSc; Fig. 44) is located at the antero-ventral part of the basal plate. The concave posterior part of BP is narrow and the posterior edge is conspicuous. The proximal part of the basal plate is flat and thus clearly distinguishable from its other parts. The antero-proximal part of the basal plate is developed as a pointy process (p in Fig. 41). The process (BPp; Fig. 43) at the ventro-proximal side of the basal plate is present but rather inconspicuous in the mesopleurum and it articulates with the pleural wing process (PWP; Figs. 43, 44).

The first free wing base sclerite (s1; Fig. 41) is long, narrow and tapered anteriorly. It articulates proximally with the ANP and distally with the second free sclerite (s2). The long and slender second free wing base sclerite (s2; Figs. 41, 42) articulates distally with the basal plate and, in addition, it is posteriorly connected to the third free wing base sclerite (s3; Figs. 41, 42). The s1 as well as the s2 are sclerotised only in the dorsal layer of the wing membrane. The third wing base sclerite (s3) is wide and conspicuous. Anteriorly, the s3 is connected (but not fused) to the basal plate. The proximal quarter of the s3 articulates with the PNP. The antero-proximal part of s3 is arched. The s3 is ventrally connected to the pleurum by the axillar-pleural muscle (Ax.PmS; Figs. 54, 55). Another, short muscle runs from the anterior part of the s3 to the postero-proximal part of the basal plate.

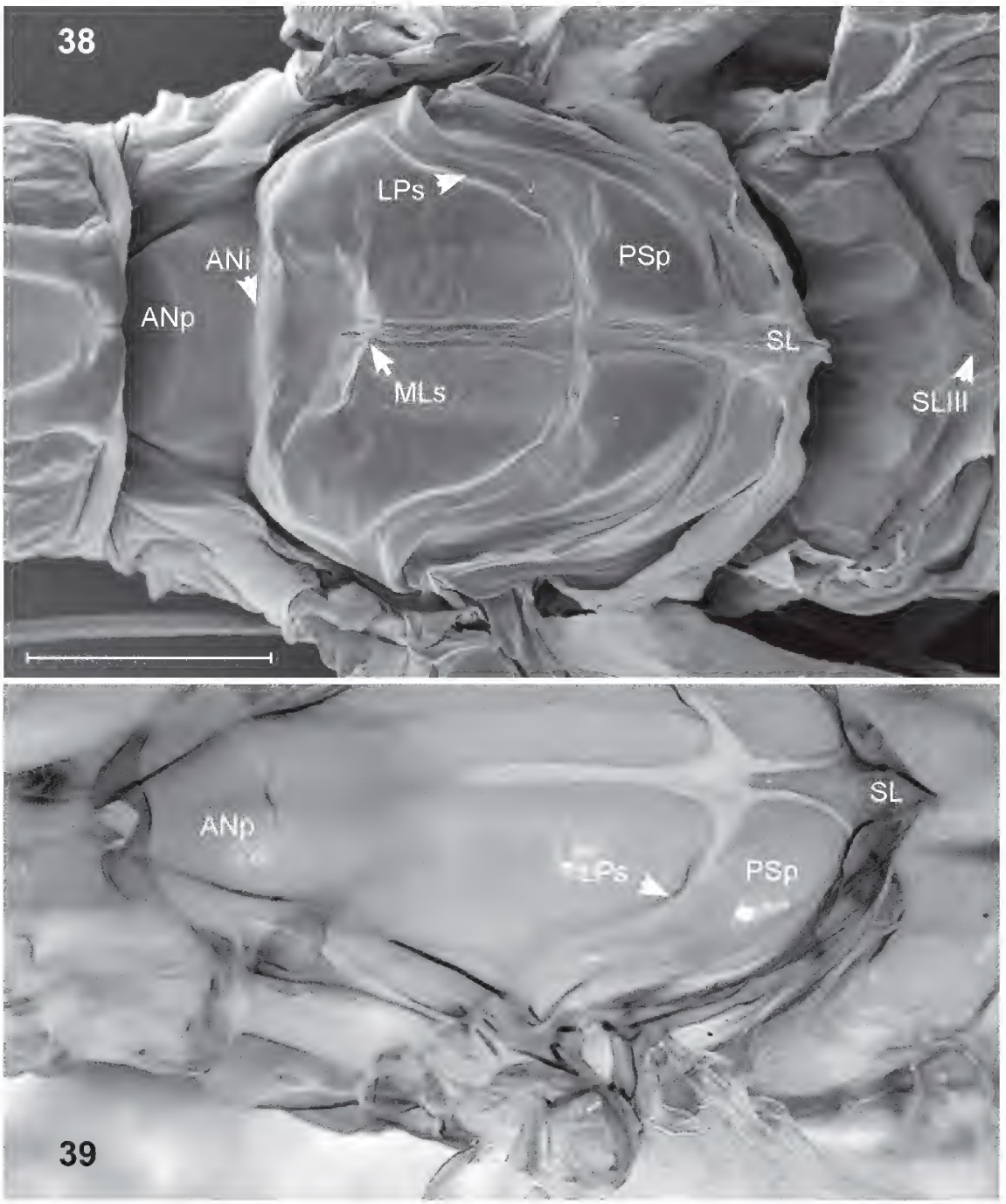
The costal brace (cb; Figs. 41, 44) and the anal brace (ab; Fig. 41) are pronounced in the wing base of *Ephoron virgo*. The costal brace connects the costal vein (C; Figs. 41, 44) with the anterior radial vein (R; Figs. 41, 42, 44). The anal brace is conspicuous and stretches between the basanale (ban; Fig. 42) and the anterior radial vein. Both the proximal (or posterior) and the distal (or anterior) arch are clearly visible. The anterior anal vein arises at the anterior part of the anal brace, next to the anterior radial vein (origin more anterior than in other Ephemeroptera). The small basanale (ban) is well sclerotised.

The anterior medial vein (MA) and the sector of the radial veins (Rs) are connected at their bases. Furthermore, the sector of the media (MP) and the anterior cubital vein (CuA) are converged at their bases.

The lateropostnotum (LPN; Figs. 43, 44) is prominent and the lateropostnotal crest (LPNC) is inconspicuous.

External morphology of the mesopleurum

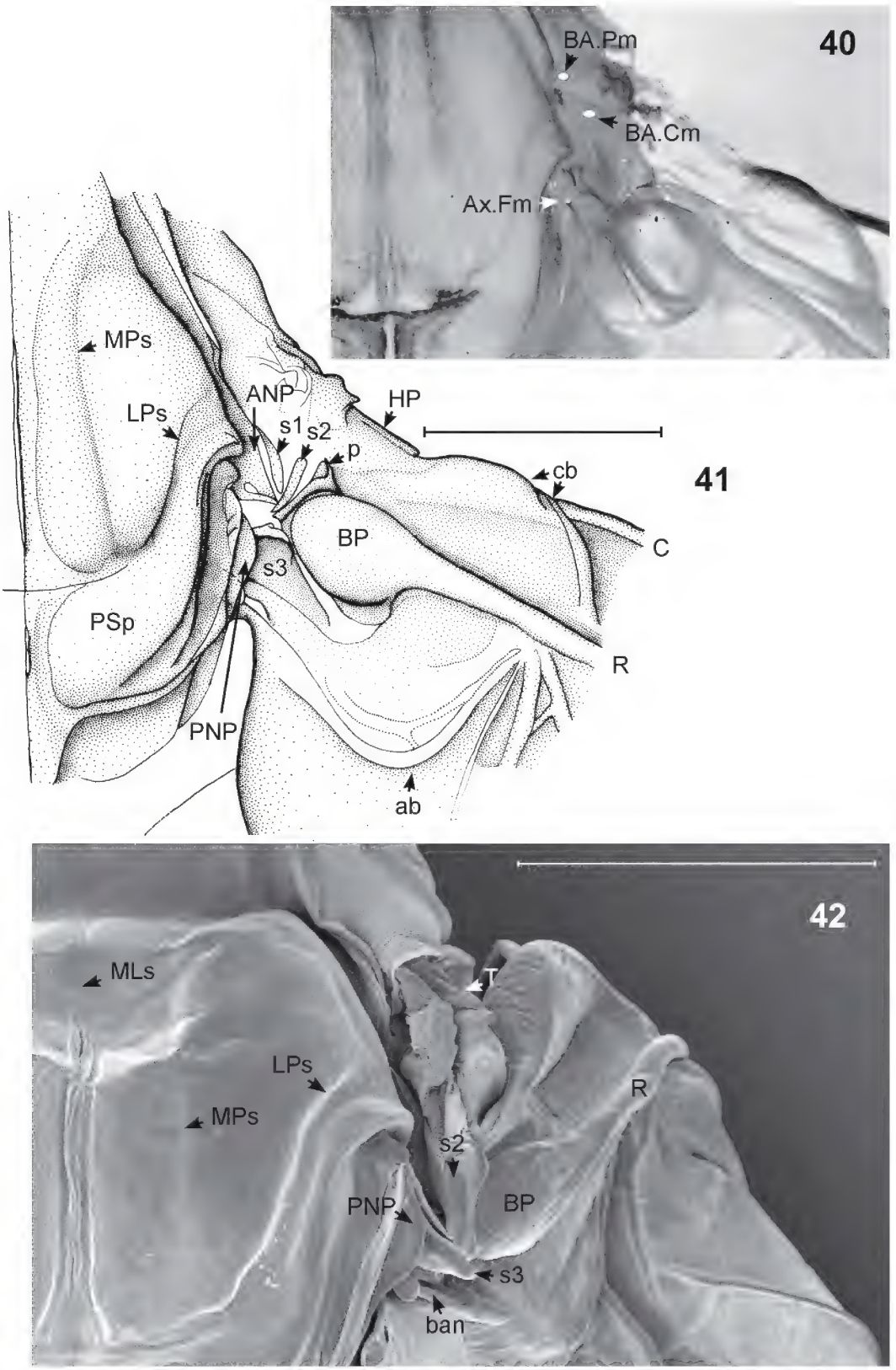
The prealar bridge is subdivided into three arcs. All three, the dorsal, ventral, and posterior arcs are long. The dorsal and the ventral arc are connected to each other. Posterior to the prealar bridge is a large membranous area with the spiracle. The spiracle is wide open in alcoholic-preserved specimens of *E. virgo* (and also in *Exeuthyplocia minima*).



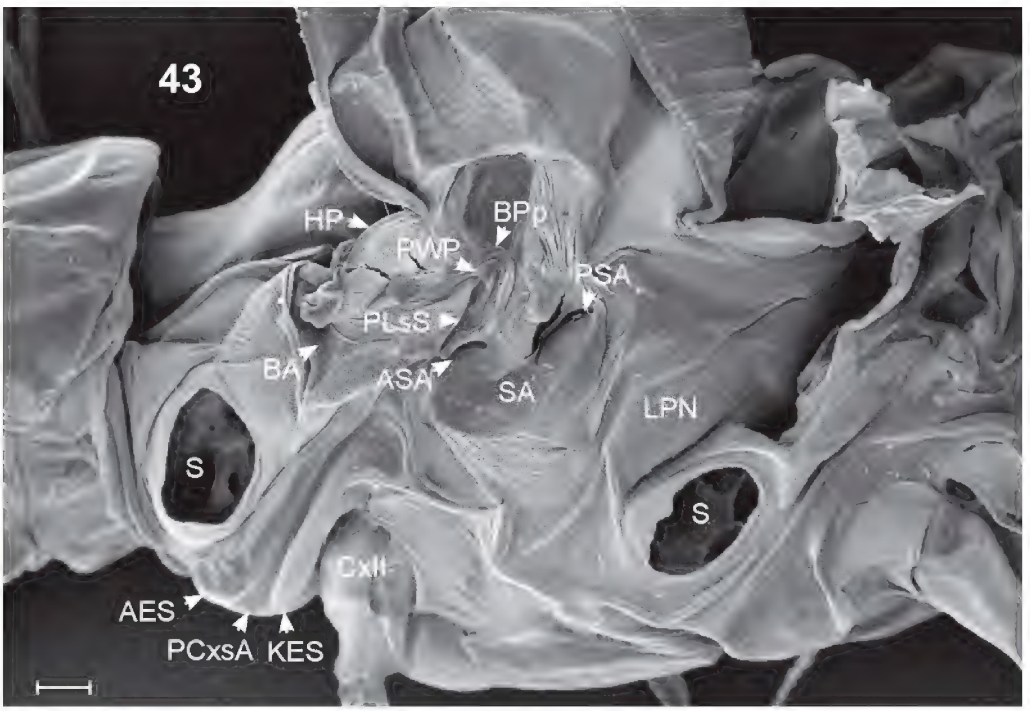
Figs. 38–39. *Ephoron virgo*, ♂ imago, mesothorax, dorsal view (head to the left). – **38**. SEM image. **39**. Mesothorax after treatment with potassium hydroxide. – Scale: 1 mm.

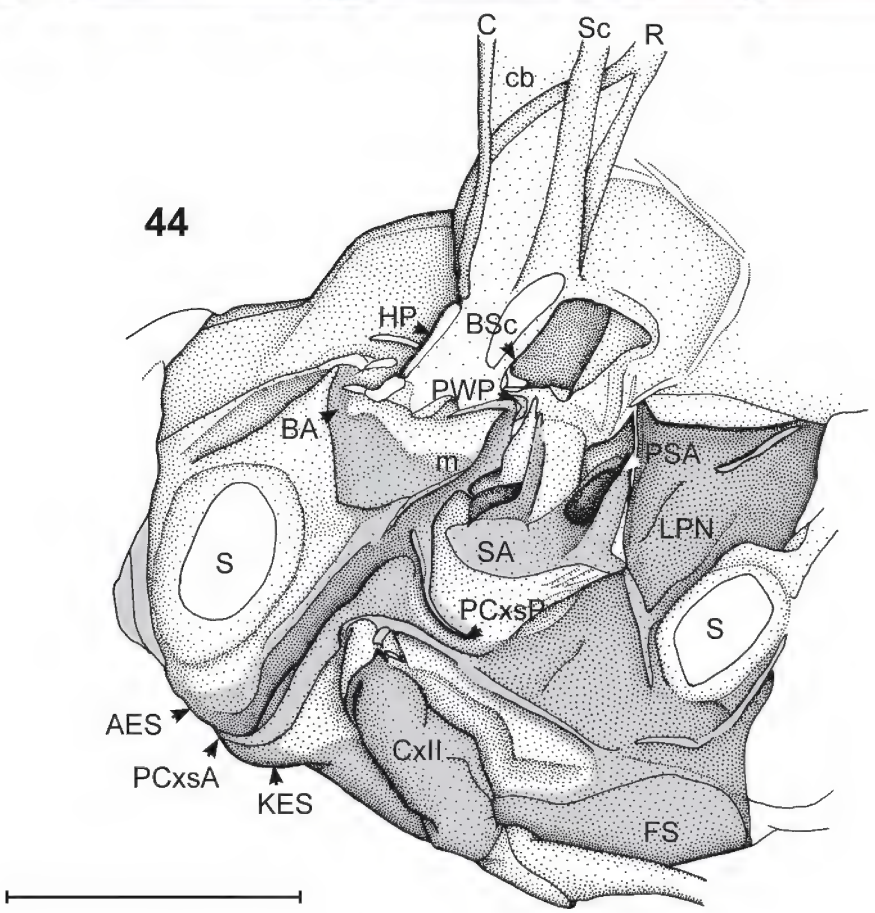
The most distinct suture in the pleurum of *E. virgo* is the anterior paracoxal suture (PCxsA; Figs. 43, 44). The PCxsA divides the anepisternum (AES; Figs. 43, 44) from the katepisternum (KES; Figs. 43, 44). Both are narrow and similar in size. The posterior part of the paracoxal suture (PCxsP; Fig. 44) is slightly less conspicuous and carinated. The upper part of the pleural suture (PLsS; Fig. 43) is conspicuous and extends dorsally into the distinct but flat pleural wing process (PWP; Figs. 43, 44). The condylus of the PWP is directed forwards. It articulates with the ventral process of the basal plate (BPp; Fig. 43) and is rather faint. The ventral part of the pleural suture (PLsI) is indistinct.

The large basalare (BA; Figs. 43, 44) at the anterior

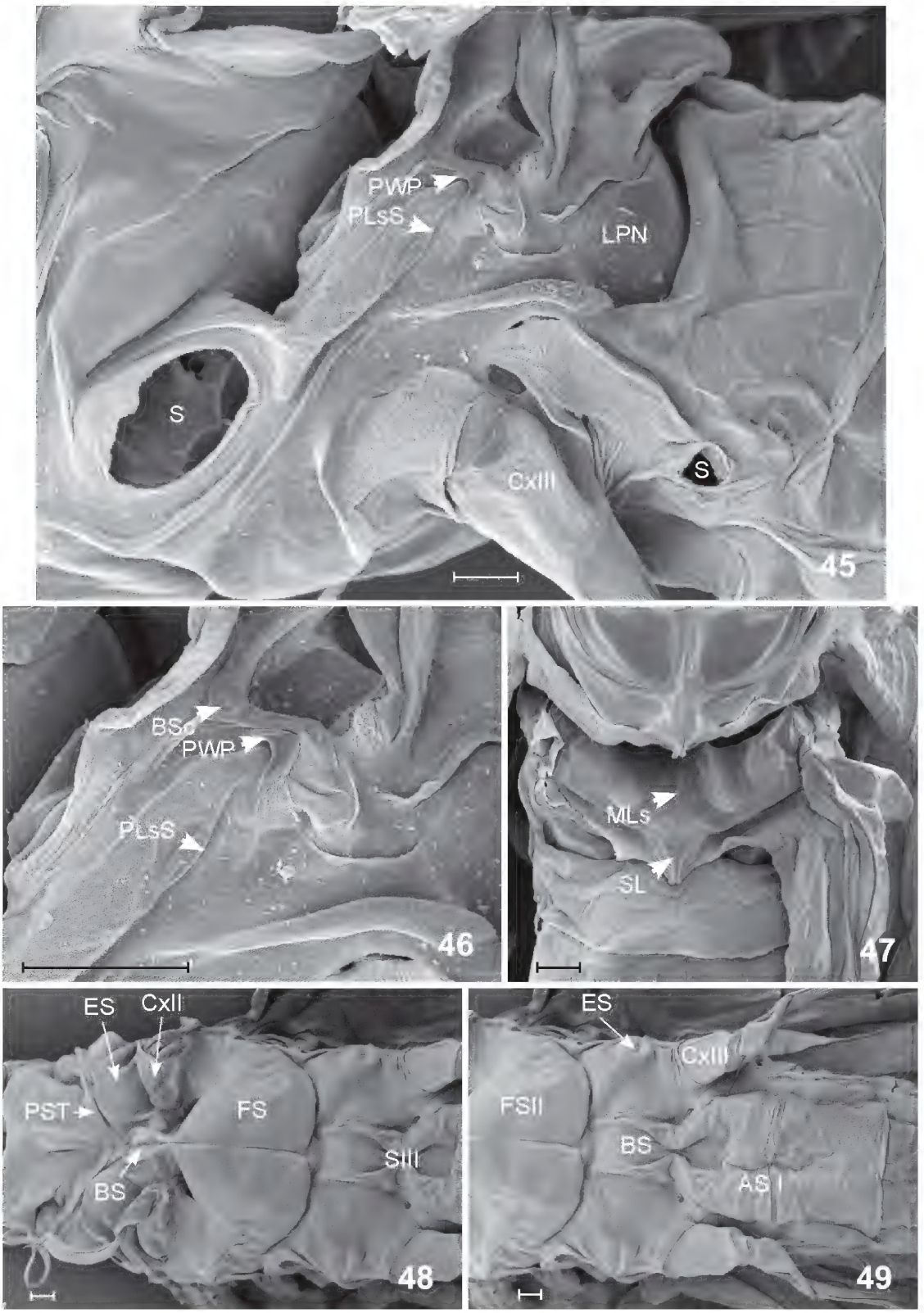


Figs. 40–42. *Ephoron virgo*, right fore wing base. – **40**. ♀, detail with the dorsal attachments of BA.Pm, BA.Cm and Ax.Fm. **41**. ♀ subimago. **42**. ♂ imago (SEM image). – p = tapered process of BP. – Scales: 1 mm.

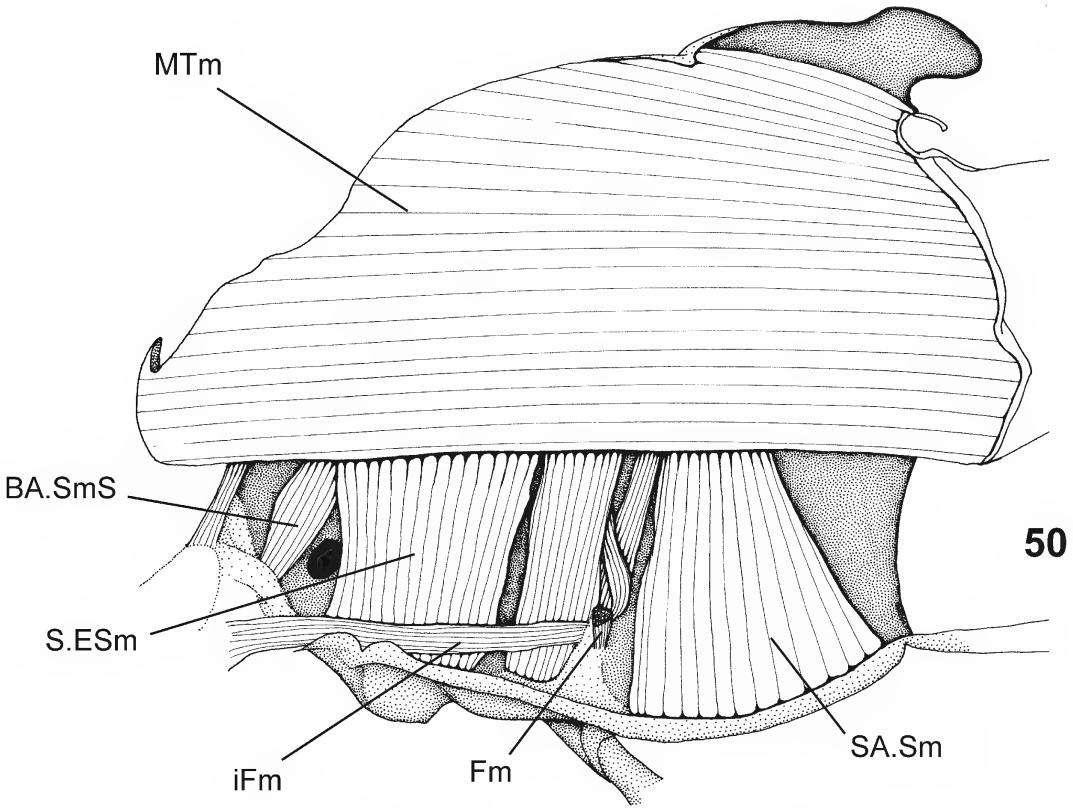


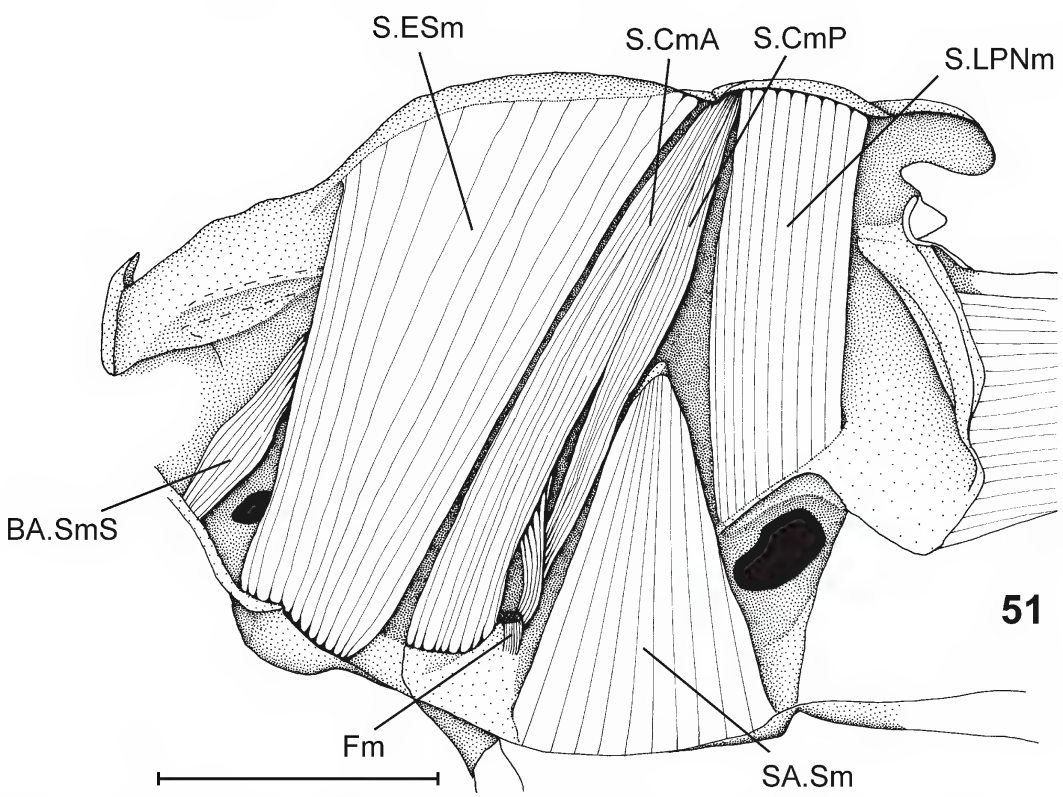


Figs. 43–44. *Ephoron virgo*, mesothorax, lateral view. – **43**. ♂ imago (SEM image). **44**. ♀ imago (grey areas sclerotised). – m = ventral attachment of BA.Pm. – Scales: 0.1 mm (43), 1 mm (44).

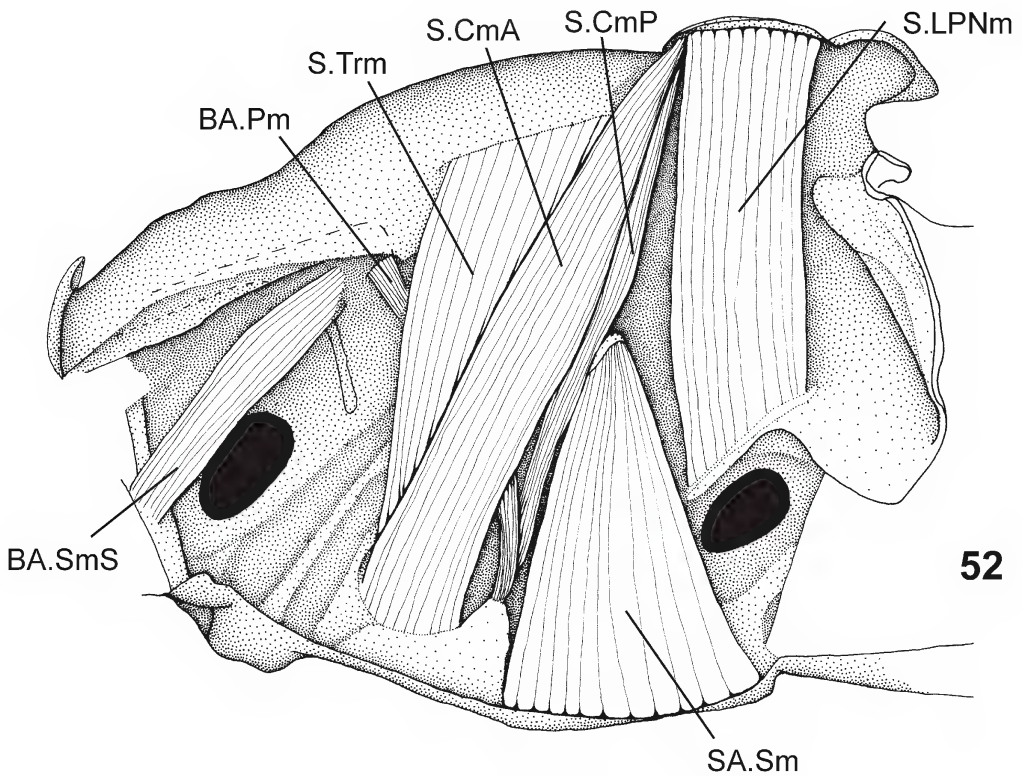


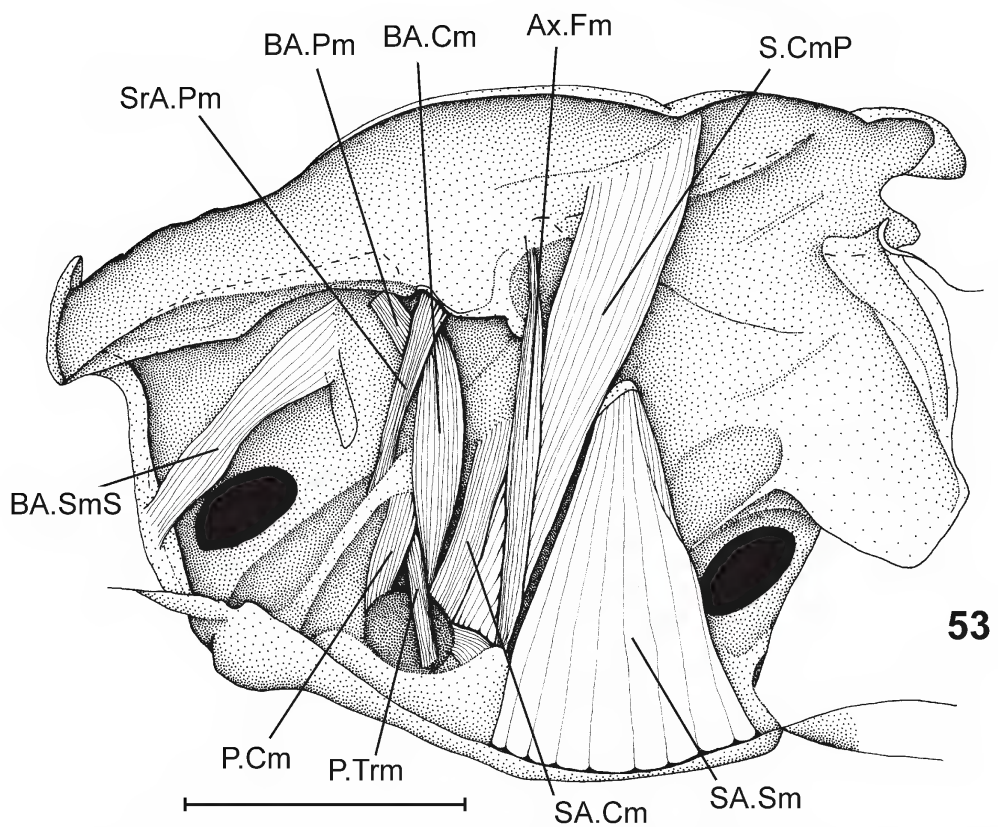
Figs. 45–49. *Ephoron virgo* (SEM images), ♂ imago. – **45**. Metathorax, lateral view. **46**. Metapleurum, upper part. **47**. Metathorax, dorsal view. **48**. Mesothorax, ventral view (head to the left). **49**. Metathorax, ventral view (head to the left). – FSII = mesothoracic furcasternum. – Scales: 0.2 mm.



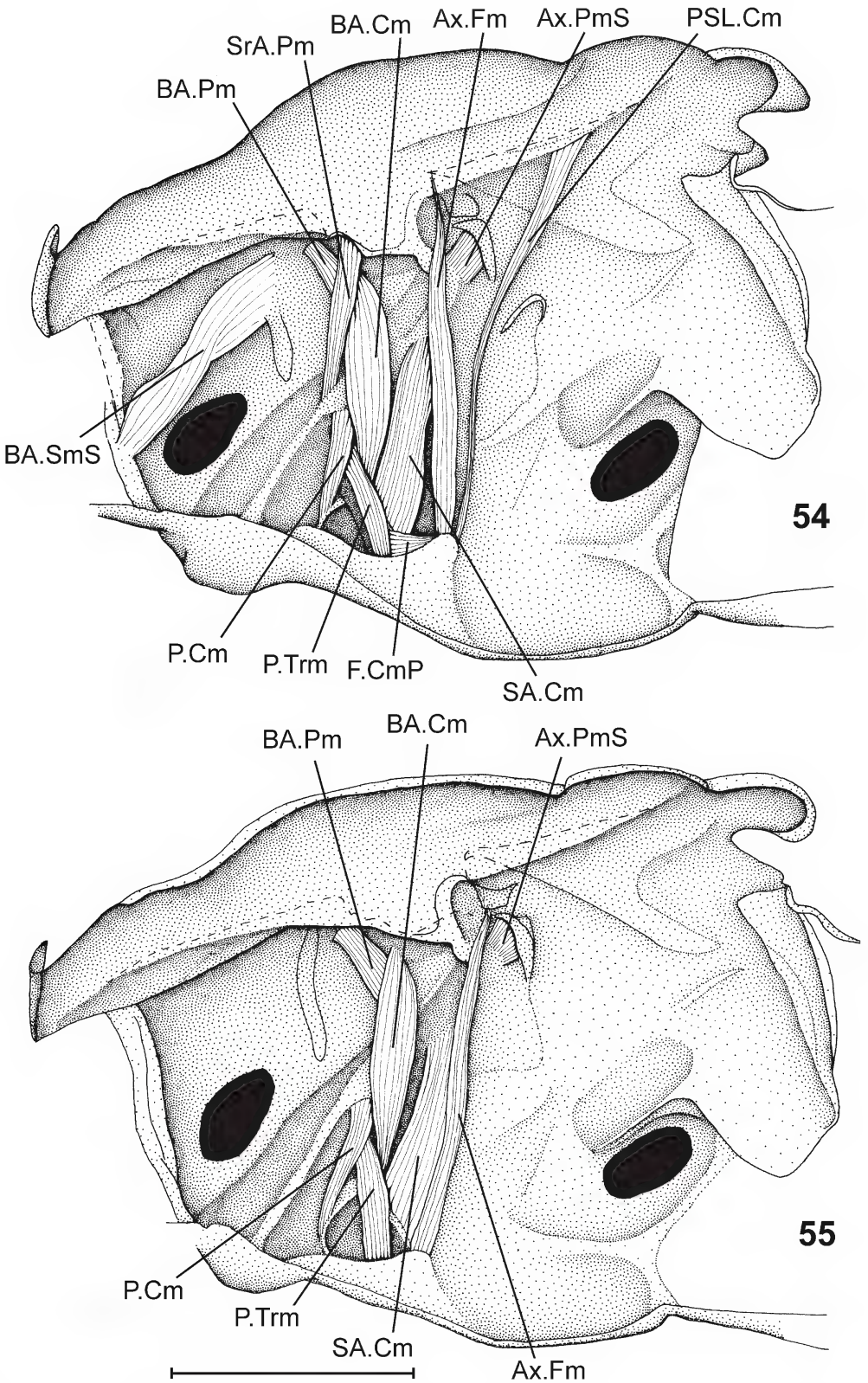


Figs. 50–51. *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (50) and progressively proceeding to the most lateral muscles (see Fig. 55). – Scale: 1 mm.





Figs. 52–53. *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 50–51). – Scale: 1 mm.



Figs. 54–55. *Ephoron virgo*, ♂ imago, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 50–51). – Scale: 1 mm.

wing base is attached to the pleurum. Posterior to the PWP lies the subalare (SA; Figs. 43, 44). The ventral part of the SA is distinct and contains the large posterior subalar apodeme (PSA; Figs. 43, 44). The dorsal part of the sclerite is slender and consists of a narrow sclerite brace and a wider ventral area. This ventral area contains the conspicuous anterior subalar apodeme (ASA; Fig. 43). The subalare is surrounded by a large membranous area.

Muscles of the mesothorax

Dorsal muscles

MTm: The median tergal muscle (Fig. 50) is large in *E. virgo* and is attached to the anterior phragma to the point of the scuto-scutellar suture and runs to the middle phragma. MTm is located medial to all other muscles.

t13: The second dorsal muscle is absent in the mesothorax.

S.LPNm: The scuto-lateropostnotal muscle (Figs. 51, 52) is dorsally attached to the posterior part of the scutum (PSp) and runs to the lateropostnotum.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle (Figs. 50, 51) runs from the scutum to the episternum. The dorsal attachment is much wider than the ventral one and extends to the lateroparapsidal suture (LPs) (laterally). It encompasses almost one half of the length of the mesothorax. The ventral point of attachment extends over the anepisternum and the katepisternum (approximately equally on each, AES and KES). The S.ESm is a bipartite muscle.

S.CmA: The anterior scuto-coxal muscle (Figs. 51, 52) stretches from the posterior part of the scutum (next to PSp) to the anterior rim of the coxa. It is a compact but rather small muscle lying postero-lateral to S.ESm.

S.CmP: The posterior scuto-coxal muscle (Figs. 51–53) is dorsally attached to the scutum (posterior to the attachment of S.CmA and anterior to S.LPNm). This flat but broad muscle proceeds to the posterior rim of the coxa.

S.Trm: The scuto-trochanteral muscle (Fig. 52) is stretched between the scutum (at the lateroparapsidal suture) and the trochanter. It is a very flat but broad muscle and is almost as large as the S.CmA.

PSL.Cm: The parascutello-coxal muscle (Fig. 54) is dorsally attached to the antero-lateral part of the scutellum and runs to the posterior rim of the coxa. The ventral point of attachment is adjacent to the attachment point of S.CmP. The PSL.Cm of *E. virgo* is rather flat and lies more anterior than PSL.Cm in other mayflies and is not visible without dissection of S.CmP.

AN.Pm: The anteronoto-pleural muscle is absent.

SrA.Pm: The suralar-pleural muscle (Figs. 53, 54) runs from the lateral part of the scutum (next to ANP) to the anterior paracoxal suture (where the PCxsP branches off). It is a flat and slender muscle that consists of only a few fibres.

Pleural muscles

P.Cm: The pleuro-coxal muscle (Figs. 53–55) is stretched between the paracoxal suture (where the anterior and the posterior suture branches off) and the antero-lateral rim of the coxa. It is a slender but robust muscle.

P.Trm: The pleuro-trochanteral muscle (Figs. 53–55) is attached to the pleural suture (above the coxo-pleural joint and near the PCxsP) and runs to the trochanter. The P.Trm lies between BA.Cm and P.Cm.

Ventral muscles

iFm: The intersegmental furcal muscle (Fig. 50) runs from the anterior part of the mesofurca to the prosternite. It is a slender muscle consisting only of a few fibres.

Fm: The slender furcal muscle (Figs. 50, 51) is stretched between the left and the right furca.

F.CmP: The flat posterior furco-coxal muscle (Fig. 54) runs from the proximal part of the mesofurca to the postero-lateral rim of the coxa.

Direct flight muscles

BA.SmS: The large superior basalar-sternal muscle (Figs. 50–54) is dorsally attached to the dorsal part of the crescent-shaped basalare and runs to the presternite.

BA.SmI: The inferior basalar-sternal muscle is absent.

BA.Pm: The basalar-pleural muscle (Figs. 40, 52–55) runs from a small sclerite of the anterior part of the wing base to the pleurum antero-ventral to the PWP.

BA.Cm: The basalar-coxal muscle (Figs. 40, 53–55) is dorsally attached (by a tendon) to a sclerite of the wing base anterior to s1. Ventrally, it is attached to the pleurum next to the coxo-pleural joint. It is a short but robust muscle.

SA.Sm: The subalar-sternal muscle (Figs. 50–53) is dorsally attached to the large posterior apodeme of the subalare (PSA) and runs to the furcasternite (Fig. 48). The muscle and its insertion area are conspicuous and large.

SA.Fm: The subalar-furcal muscle (not pictured) is slender and inconspicuous and stretches between the tip of the subalar apodeme (PSA) and the furca (or next to it, so that it is attached to the posterior rim of the coxa).

SA.Cm: The robust subalar-coxal muscle (Figs. 53–55) inserts on the anterior subalar apodeme (ASA) and runs to the postero-lateral rim of the coxa.

Ax.Fm: The axillar-furcal muscle (Figs. 40, 53–55) is dorsally attached to the PNP (in contrast to other

Ephemeroptera) and runs to the furca. The muscle is larger than in other Ephemeroptera.

Ax.PmI: The (inferior) axillar-pleural muscle is not present in *Ephoron virgo*.

Ax.PmS: The (superior) axillar-pleural muscle (Figs. 54, 55) is a short but robust muscle running from the third axillary sclerite to the antero-dorsal part of the subalare (and the membrane between this part of the SA and the PWP). A second and smaller part of this muscle is attached to the third axillary sclerite and runs to the postero-proximal part of the basal plate.

External morphology of the metanotum

The metanotum is shortened. The scutum is about three times as long as the scutellum (SL; Fig. 47). Nevertheless, the dorsal part of the scutellum is, in relation to the mesothorax, quite long. The sutures (except MLs; Fig. 47) and convexities of the metanotum are rather indistinct.

The ANP and the PNP (not pictured) are conspicuous even in the metathorax. The basal plate (BP, not pictured) of the wing base is prominent and the proximal flat part clearly distinguishable from its other parts. A short process lies at the antero-proximal margin. The posterior part of BP is connected to the third wing base sclerite (s3). The first free wing base sclerite (s1) is long and narrow and articulates with the ANP. The second wing base sclerite (s2) is not visible in the metathoracic wing base. At the posterior part of the BP lies the third wing base sclerite (s3). It is a distinct sclerite that articulates with the BP distally and with the PNP proximally. The ban is also visible in the metathoracic wing base.

External morphology of the metapleurum
(Figs. 45, 46)

The sutures and sclerites are partly or completely reduced in the metathorax. The upper part of the pleural suture (PLsS) is conspicuous and runs obliquely towards the head (dorso-ventrally). The PLsS extends dorsally into the distinct PWP. The condylus of PWP is conspicuous and almost as large as the condylus of the mesothorax. It is also rather flat. It articulates with the proximal base of the basal plate (BP). The inferior part of the pleural suture (PLsI) is inconspicuous.

The basalare, anterior to the PWP, is not present in the metapleurum. Rudimental parts of the subalare are present posterior to the PWP.

The anterior paracoxal suture (PCxsA) is clearly visible even in the metathorax. The lateropostnotum (LPN) is conspicuous.

Muscles of the metathorax

Dorsal muscles

MTm: The median tergal muscle runs from the middle phragma to the posterior phragma. It is a relatively short but robust muscle that is somewhat smaller than the metathoracic MTm of other mayflies.

t13: The second dorsal muscle is absent from the metathorax.

S.LPNm: The scuto-lateropostnotal muscle was not found.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle is dorsally attached to (about one third!) of the scutum and runs to the episternum. It is a very large muscle in the metathorax that is of similar size as the MTm of the metathorax (distinctly larger than the S.ESm of the metathorax of other mayflies, e. g. *Siphlonurus aestivalis*, *Baetis* sp., *Serratella ignita*, *Habroleptoides confusa* etc.).

S.CmA: The anterior scuto-coxal muscle is dorsally attached to the scutum and ventrally to the anterior rim of the coxa. It is a slender muscle that is slightly stronger than the S.Trm.

S.CmP: The posterior scuto-coxal muscle stretches from the posterior part of the scutum to the posterior rim of the coxa. It is a slender muscle, which is slightly stronger than the S.CmA and the S.Trm (S.CmP > S.CmA > S.Trm). S.CmP apparently consists of two parts. The second part is about half in size as the first part.

S.Trm: The scuto-trochanteral muscle is dorsally attached to the posterior part of the scutum and proceeds to the trochanter.

PSL.Cm: The parascutello-coxal muscle is either reduced in the metathorax or it is also possible that PSL.Cm is the second part of S.CmP and is shifted anteriorly.

AN.Pm: The anteronoto-pleural muscle runs from the antero-dorsal part of the metathorax to the pleural suture (where PCxsA, PCxsP and PLs converge). It is a flat and weak muscle.

SrA.Pm: The suralar-pleural muscle is a slender muscle running from the antero-lateral part of the scutum to the anterior paracoxal suture. It consists of only a few fibres.

Pleural muscles

P.Cm: The flat pleuro-coxal muscle runs from the anterior paracoxal suture (PCxsA) to the anterior rim of the coxa. It is a broad and robust muscle.

P.Trm: The pleuro-trochanteral muscle is attached to the anterior paracoxal suture (PCxsA) and runs to the trochanter. It is a conspicuous muscle lying posterior to P.Cm.

Ventral muscles

iFm: A slender muscle, located roughly in the same position as the intersegmental furcal muscle.

Fm: The furcal muscle is stretched between the left and the right metafurca. It is a conspicuous muscle, although the metafurca is small and indistinct.

F.CmP: The posterior furco-coxal muscle is a flat muscle running from the short furca to the lateral rim of the coxa.

Direct flight muscles

BA.SmS/BA.SmI: The superior and the inferior basalar-sternal muscles are not present in the metathorax.

BA.Pm: The basalar-pleural muscle runs from the scutum to the pleurum (anterior to the PWP). It is a flat and broad muscle, which is large in comparison to the mesothoracic BA.Pm.

BA.Cm: The basalar-coxal muscle is dorsally attached to the part of the wing base that is proximal to the s1. Ventrally, it is attached to the lateral rim of the coxa. It is a distinct muscle (stronger than S.CmP).

SA.Sm/SA.Fm/SA.Cm: The subalare of the metathorax is reduced to an indistinct sclerite. The subalar muscles are also reduced in the metathorax; the subalar-sternal muscle and the subalar-furcal muscle are partly or completely reduced (there is no muscle left running to the sternum or to the furca). One flat but robust muscle is dorsally attached to the pleurum (to the remains of a subalar apodeme/subalar sclerite). Ventrally, it is attached to the postero-medial rim of the coxa.

Ax.Fm: The axillar-furcal muscle is a slender but conspicuous muscle running from a sclerite of the wing base to the furca.

Ax.PmS: A muscle, possibly superior axillar-pleural one, is present running from the postero-lateral part of the scutum (at the same level as s3) to the pleurum posterior to the PWP. It is a flat muscle consisting of only a few fibres.

Ax.PmI: The (inferior) axillar-pleural muscle is absent.

3.2.5 *Baetis* sp., late larvae (Figs. 56–57) (n = 4)

External morphology of the mesonotum

The notum of the mesothorax is much larger than the notum of the metathorax. The median longitudinal suture (MLs) is conspicuous over the whole length of the notum. This is the suture where the cuticula ruptures during ecdysis. The medioparapsidal sutures (MPs) and the lateroparapsidal sutures (LPs) are rather indistinct. The anterior part of the scutum (ANp, ANi) is not clearly differentiated. The middle part of the scutum and the posterior scutal protuberances (PSp), as well as the scutellum are conspicuous. The wing pads are located at the lateral parts of the tergum. No elements of the wing base are differentiated in earlier larval stages. The metanotum is short and without any obvious differentiations.

External morphology of the mesopleurum (Fig. 56)

All three pairs of legs are well differentiated since they are important for locomotion in the larval stages. The mesothorax is not as differentiated as in the winged stages. Both the mesopleurum and the metapleurum are about equal in dimension. The pleurum consists of the simple anterior episternum and the posterior epimeron, which are separated by the pleural suture.

Muscles of the mesothorax (Fig. 57)

The dimensions of the pterothoracic muscles are not equivalent to the winged stages. The dorsal longitudinal muscle (MTm) is weak in earlier larval stages since the phragmata are not differentiated yet. The S.ESm is always a comparatively large muscle, at least in the mesothorax. The remaining dorso-ventral muscles are slender and almost equal in size. The S.CmP is much smaller in the metathorax than in the mesothorax in earlier larval stages. A weak muscle is present in both meso- and metathorax, which is stretched between a small sclerite in the anterior membrane of the pleurum (next to the stigma) and the presternite. Several muscles are present only in the larval stages.

Dorsal muscles

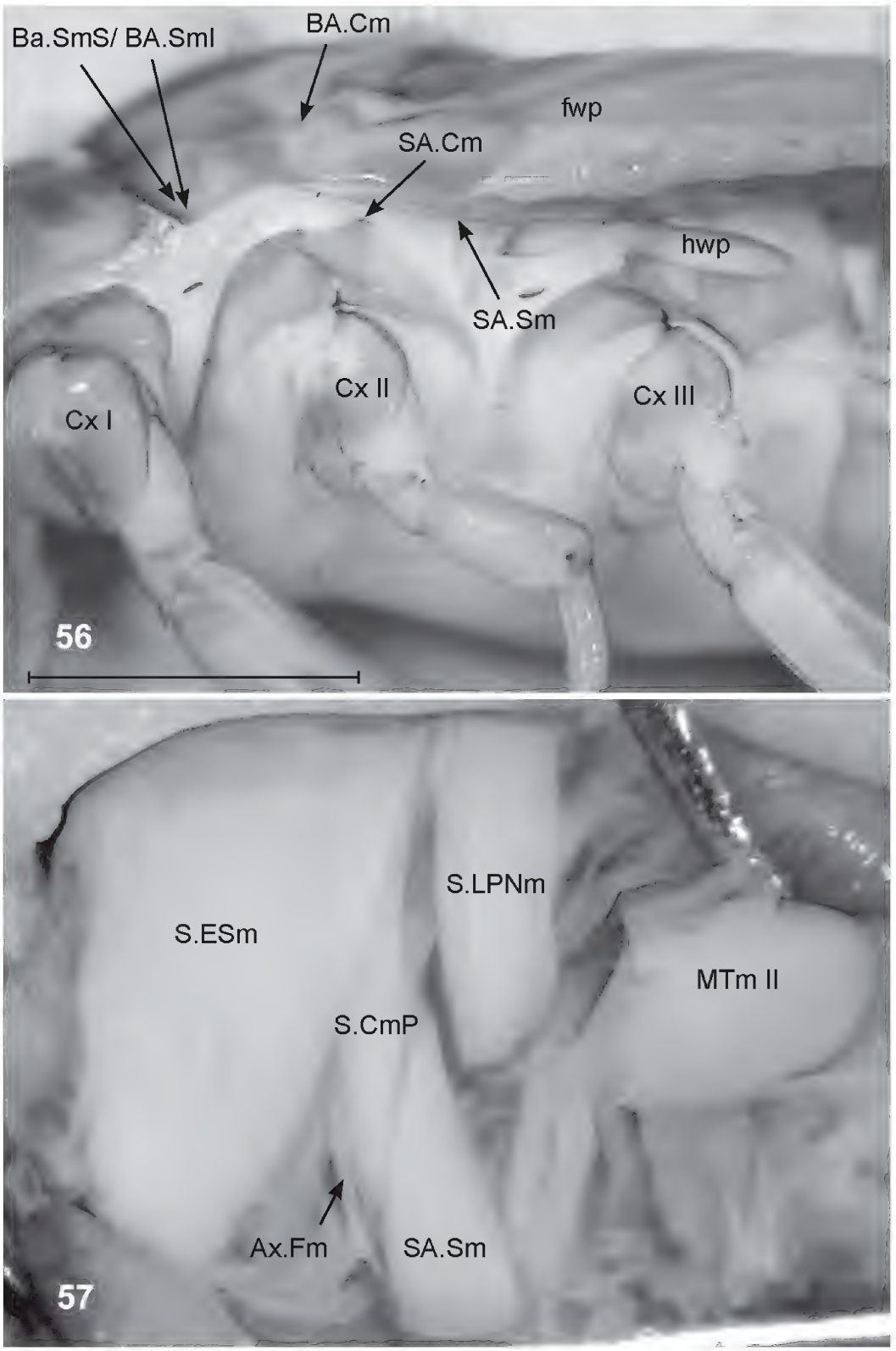
MTm: The median tergal muscle stretches from the middle phragma to the posterior phragma. It is a flat muscle, which is not enlarged as it is in subimaginal and imaginal Ephemeroptera. The height of MTm is less than one half of the height of the mesothorax (in a late larval stage).

t13: The second dorsal muscle stretches from the posterior part of the scutum to the posterior phragma. It is small and slender but distinct.

S.LPN.m: The scuto-lateropostnotal muscle is dorsally attached to the posterior part of the scutum (or posterior scutal protuberance, PSp) lateral to t13 and proceeds to the lateropostnotum. It is a short, flat and small muscle, which becomes much larger in winged stages.

Dorso-ventral muscles

S.ESm: The scuto-episternal muscle runs from the anterior part of the scutum to the anterior rim of the pleural sclerit, i. e. the episternum. The dorsal point of attachment of the S.ESm is the second widest attachment of the mesothoracic muscles. It encompasses almost one half of the scutum length. Ventrally, the muscle becomes more slender.



Figs. 56–57. *Baetis* sp., late larva, same specimen, lateral view. – **56**. Mesopleurum and metapleurum; the arrows show the attachment of the basalar and the subalar muscles. **57**. Musculature of the right half of the mesothorax, showing the large S.ESm and the small SA.Sm. – Scale: 1 mm.

S.CmA: The anterior scuto-coxal muscle is dorsally attached to the scutum (lateral to the lateroparapsidal suture, LPs) and runs to the anterior rim of the coxa. The dorsal attachment of this muscle lies latero-ventral to that of S.ESm. The S.CmA is a flat and slender muscle and seems to consist of two parts.

S.CmP: The posterior scuto-coxal muscle is dorsally attached to the posterior part of the scutum and runs to the posterior rim of the coxa. The S.CmP is slightly larger than the S.CmA.

S.Trm: The scuto-trochanteral muscle running from the scutum (antero-medial to the Ax.Fm) to the trochanter is a very large muscle. It is larger than the S.CmP and the S.CmA.

PSL.Cm: The parascutello-coxal muscle runs from the anterior part of the scutellum to the posterior rim of the coxa. It is distinct and larger than the PSL.Cm of subimagines and imagines.

AN.Pm: The anteronoto-pleural muscle stretches from the antero-lateral part of the notum to the anterior paracoxal suture (PCxsA, anterior rim of the pleural sclerite, which is well sclerotised). It is a clearly visible but flat muscle consisting only of a few fibres.

SrA.Pm: The suralar-pleural muscle runs from the lateral part of the scutum to the pleurum above the attachment of AN.Pm.

Pleural muscles

P.Cm: The pleuro-coxal muscle is dorsally attached to the anterior rim of the pleurum and ventrally to the anterior coxal rim. It is a short, flat and broad muscle, which is almost oval in cross section.

P.Trm: The pleuro-trochanteral muscle stretches between the pleural suture (above the coxal articulation) and the trochanter. It is a robust muscle, which is almost round in cross section and gets broader ventrally.

Ventral muscles

iFm: The intersegmental furcal muscle runs from the anterior side of the mesofurca to the posterior part of the prothoracic furca.

Fm: The short but robust furcal muscle stretches between the proximal side of the right furca and the proximal side of the left furca.

F.CmP: The posterior furco-coxal muscle, which runs from the furca to the posterior rim of the coxa, is a distinct and robust muscle.

Future direct flight muscles

BA.SmS: There is one broad muscle in a position similar to BA.SmS and BA.SmI of the thorax of adult stages. Most likely the superior basalar-sternal muscle and the inferior basalar-sternal muscle (**BA.SmI**) run parallel in close proximity to each other in larvae of *Baetis* sp. The muscles are dorsally attached to the antero-lateral part of the scutum and ventrally to the furca of the prothorax.

BA.Pm: The basalar-pleural muscle is dorsally attached to the scutum (posterior to the BA.Sm and lateral to the SrA.Pm). It proceeds to the pleural membrane directly below the anterior part of the fore wing pad.

BA.Cm: The basalar-coxal muscle is dorsally attached to the scutum (posterior to the BA.Pm) and runs to the coxo-pleural joint.

SA.Sm: The subalar-sternal muscle is dorsally attached to a small sclerite in the pleural membrane (below the posterior part of the fore wing pad) and runs to the sternum. It is only a slender muscle in contrast to the SA.Sm of subimagines and imagines (Fig. 57).

SA.Fm: The flat and slender subalar-furcal muscle is dorsally attached to the same sclerite as the SA.Sm. Ventrally, it is attached to the furca of the mesothorax.

SA.Cm: The subalar-coxal muscle runs from the pleural sclerite (postero-dorsal edge of the pleural sclerite, the epimeron) to the postero-lateral rim of the coxa.

Ax.Fm: The axillar-furcal muscle is stretched between the scutum (slightly posterior to the BA.Cm) and the furca. It is a slender muscle and is almost as large as the mesothoracic Ax.Fm of the winged stages.

Muscles of the metathorax

Dorsal muscles

MTm: The median tergal muscle is anteriorly attached to the middle phragma and posteriorly to the posterior phragma. It is rather small in relation to the MTm of subimagines and imagines.

t13: This short and weak muscle is stretched between the posterior part of the notum and the upper part of the posterior phragma.

S.LPN.m: The scuto-lateropostnotal muscle is absent in the metathorax.

Dorso-ventral muscles

S.ESm: The slender scuto-episternal muscle is dorsally attached to the anterior part of the scutum and ventrally to the anepisternum (more lateral than in the mesothorax).

S.CmA: The anterior scuto-coxal muscle runs from the antero-lateral part of the scutum to the anterior coxal rim. It is a flat, broad muscle and smaller than both the S.CmP and the S.Trm.

S.CmP: The posterior scuto-coxal muscle is dorsally attached to the middle part of the scutum (posterior to the S.Trm) and runs to the posterior coxal rim.

S.Trm: The scuto-trochanteral muscle is dorsally attached to the middle part of the scutum (lateral to S.CmA and

S.CmP) and runs to the trochanter. S.Trm is considerably larger than S.CmA and S.CmP.

PSL.Cm: The parascutello-coxal muscle is a slender muscle that stretches between the posterior area of the notum and the posterior rim of the coxa.

SrA.Pm: The suralar-pleural muscle is a flat and relatively broad muscle running from the lateral part of the scutum to the anterior rim of the pleural sclerite next to the dorsal attachment of the SA.Cm. A weak and narrow muscle diverges from the SrA.Pm and runs to the pleural sclerite posterior to the SrA.Pm.

Pleural muscles

P.Cm: The pleuro-coxal muscle is a flat but wide muscle running from the pleurum (PCxsA, anterior rim of the pleural sclerite) to the anterior coxal rim. It is a broad but flat muscle, which consists only of a few fibres.

P.Trm: The pleuro-trochanteral muscle is dorsally attached to the anterior rim of the pleural sclerite (PCxsA), posterior to P.Cm, and runs to the trochanter. It is a robust muscle that is almost round in cross section.

Ventral muscles

iFm: The flat and broad intersegmental furcal muscle runs from the anterior part of the metafurca to an apodeme directly posterior to the mesofurca.

Fm: The furcal muscle joins the left and right metafurcal branches. It is elliptic in cross section.

F.CmP: The posterior furco-coxal muscle runs from the furca to the posterior rim of the coxa (medial to the ventral attachment point of SA.Cm). It is a distinct flat muscle.

Future direct flight muscles

The basalar muscles are most likely absent in the metathorax but the small muscle that diverges from the SrA.Pm and runs to the pleurum is probably the **BA.Pm**.

The two subalar-sternal muscles (**SA.Sm** and **SA.Fm**) are missing in the metathorax.

SA.Cm: The subalar-coxal muscle is flat and runs from the pleurum (process at the pleural suture) to the posterior rim of the coxa.

Ax.Fm: The slender axillar-furcal muscle is dorsally attached to the lateral part of the scutum and ventrally to the furca.

Further larval muscles

A flat muscle stretches between the anterior phragma and the posterior part of the second abdominal segment. Ventrally, there is a second muscle, which runs to the posterior part of the second abdominal segment. Both muscles are flat, broad and bipartite. Each of the second parts is attached to the anterior part of the second abdominal segment.

Furthermore, a tendon-like, slender and flat muscle is stretched between the anterior phragma and the anterior rim of the coxa. It is a weak muscle that consists of only a few fibres. It is present in the mesothorax and the metathorax.

Two flat and broad muscles are attached to the furca of the metathorax. The first muscle runs to the anterior part and the second one to the posterior part of the first abdominal segment.

A flat muscle stretches between the posterior phragma and the first abdominal segment.

A further slender muscle is attached to the posterior phragma and to the sternum (just anterior to the metasternum).

A narrow muscle stretches between the anterior part of the first abdominal tergite and the posterior rim of the coxa.

3.3 Odonata
(Figs. 58–66)

3.3.1 General Remarks

The pterothorax of Odonata is specialised and adapted to their hunting behaviour. The mesothorax and metathorax are large and directed obliquely forwards, relative to the small and simple prothorax. The orientation of the pterothorax together with the orientation of the legs forms a characteristic capture apparatus. Most of the flight muscles are direct acting muscles.

3.3.2 *Sympetrum* cf. *striolatum*
(n = 1)

Measurements (♂)

Total length: 38 mm. – Length of mesothorax: 3.6 mm. – Length of mesothoracic wing: 29 mm. – Width of mesothoracic wing: 7 mm. – Length of metathorax: 3.4 mm. – Length of metathoracic wing: 28 mm. – Width of metathoracic wing: 9 mm.

External morphology of the mesonotum

The pterothoracic notal elements are strongly reduced in Odonata. The anterior area of the notum is the conspicuous prescutum (following Asahina 1954), which is demarcated from the scutum (S; Fig. 58). The lateral part of the prescutum (PRS; Fig. 58) is located between the scutum and the humeral plate (hp; Fig. 58). PRS is anteriorly tightly associated with the humeral plate. It is the dorsal attachment of the short muscle 28. A further narrow sclerite, lying in-between the lateral part of the prescutum and the humeral plate, serves as the dorsal attachment for the muscle 26. The latter two sclerites have been assumed

to be the 1Ax (Pt 1 sensu TANNERT 1958). The scutum is a large convex sclerite with the associated internal tergal apophysis, which serves as attachment of the muscle 23. The convex scutal sclerite and the tergal apophysis are larger in the metathorax than in the mesothorax.

The fore and hind wings articulate with the tergum via two large plates. The anterior humeral plate (hp) articulates proximally with the prescutum and distally with the costal vein of the wing. Two muscles, 21 and 22, are attached to the lateral margin of the humeral plate. Furthermore, hp is associated with the anterior part of the pleural wing process (PWP; Figs. 59, 60). Posterior to the humeral plate lies the axillary plate (axp; Fig. 58). The anterior radial vein (R; Fig. 58) and the anterior medial vein (MA; Fig. 58) originate from the anterior part of axp. The sector of the medial vein (MP; Fig. 58) and the cubital vein (Cu; Fig. 58) are connected to the posterior part of the axillary plate. Furthermore, the anterior part of the axp is connected to the posterior pleural wing process (PWP; Figs. 59, 60). Five muscles are associated with the axillary plate: 27, 29, 32, 33 and 34. The antero-ventral part of the axillary plate serves as the dorsal attachment of muscles 27 and 32. Both muscles, 33 and 34, are indirectly connected to the postero-ventral part of the axillary plate. The short and bipartite muscle 29 is attached to the posterior part of the axillary plate and proceeds to the pleurum.

External morphology of the mesopleurum

The pleurum of Odonata is specialised, since the meso- and metapleurum are fused to each other. The anterior parts of the right and the left episternites are connected to each other and separated by a dorsal carina. The episternum (ES; Fig. 59) is a large sclerite that is separated from the epimeron (EM; Fig. 59) by the pleural suture (PLs; Figs. 59, 60). The conspicuous pleural suture extends dorsally into the distinct posterior pleural wing process (PWP; Figs. 59, 60) of the mesothorax that articulates with the anterior part of the axillary plate (axp). The upper part of the mesothoracic epimeron is fused to the metathoracic episternum. The area anterior and posterior to the posterior pleural wing process is membranous. A small sclerite (s in Fig. 60) is visible in the upper third of the membrane posterior to the posterior PWP. It is the dorsal attachment of the muscles 33 and 34. The epimeron is only ventrally separated from the metathoracic episternum by the interpleural suture (following ASAHINA 1954).

Muscles of the mesothorax (Figs. 61–66)

The muscles of mesothoracic origin are arranged after the numbers of ASAHINA (1954); the corresponding muscles of metathoracic origin are given in parentheses.

The muscles 24 and 35 are absent in *Sympetrum* cf. *striolatum* and, according to ASAHINA (1954) and MALOEUF (1935), also in all other adult Odonata. According to ASAHINA muscle 31 is present in *Epiophlebia*, *Davidius*, and *Mnais*; it is, however, absent in *Sympetrum* cf. *striolatum* and, according to MALOEUF, in adult Odonata. Muscle 37 is present in *S.* cf. *striolatum* and, according to ASAHINA, also in *Epiophlebia* and *Davidius*. In contrast, according to MALOEUF, muscle 37 is absent in adult Odonata.

21 (43): The sternopleural/sternobasalar muscle is small and short. It is dorsally attached by a long tendon to the antero-lateral part of the humeral plate. The ventral attachment lies just lateral to muscle 22. In the metathorax, it is dorsally attached to the antero-lateral part of the humeral plate via a tendon. Ventrally, it is attached to the preepisternum (near the stigma), also by a tendon. It is not as closely associated with the larger muscle (44) as the corresponding muscle of the mesothorax to muscle 22.

22 (44): The large sternopleural/sternobasalar muscle is dorsally attached to the antero-lateral part of the humeral plate via a tendon that is sclerotised basally. A second branch of this tendon runs to the centre part of the humeral plate. Ventrally, muscle 22 is attached to the preepisternal apodeme (sensu ASAHINA 1954). The muscle is bipartite and the dorsal apodeme has a gap in the anterior area. The ventral apodeme that serves as attachment of the metathoracic sternobasalar muscle (44) is not as mobile as in the mesothorax.

23 (46): The large anterior tergosternal muscle is dorsally attached to the tergum. Ventrally, it attaches to an apodeme that runs to the antero-medial rim of the coxa. An apodeme-like sclerite, which is tightly connected to a bullous arched part of the tergite serves as the dorsal attachment.

23′ (46′): Lateral to the anterior tergosternal muscle 23 lies a smaller and shorter muscle (23′), which is dorsally and ventrally attached to the same points as muscle 23. It is ventrally attached by a long tendon.

25 (45): The dorsal longitudinal muscle is attached to the tergal apophysis (anterior phragma) and to the lateral part of the notum just between the meso- and metathorax. This rather small and weak muscle is present in the mesothorax, but absent in the metathorax.

26 (48): The coxobasalar muscle is dorsally attached to a tergal sclerite via a tendon, which is distally connected to the humeral plate. It runs to the pleural ridge next to the postero-lateral rim of the coxa. The muscle 26 is a rather narrow muscle and smaller than muscle 27.

27 (49): The dorsal attachment of the coxosubalar muscle lies postero-medial of muscle 26. It is dorsally attached to the antero-proximal part of the axillary plate and proceeds to the pleural ridge next to the postero-lateral rim of the coxa. A second part is stretched between the same attachments of the first part, but dorsally it is attached via an apodeme.

28 (50): The short but robust tergopleural muscle is dorsally attached to the prescutum (PRS; Fig. 58) and ventrally to the upper part of the pleural ridge.

29/30 (51/52): Both pleuroaxillary muscles (or rather one bipartite muscle) are attached to the posterior part of the axillary plate and proceed to a narrow sclerite of the pleurum posterior to the PWP. The pleural sclerite is tightly connected to the PWP. The two parts of the muscles are better distinguishable in the metathorax. The distal part of the metathoracic muscles is attached to an indistinct pleural sclerite posterior to the PWP. It is almost round in cross section. The proximal part is wider but flat and runs to a sclerite of the pleurum that is tightly associated with the PWP similar to the mesothoracic sclerite. Nevertheless, the connection between the muscle and the sclerite is stronger in the metathorax.

31 (53): This pleuroaxillary muscle is absent in *Sympetrum* (missing in adult Odonata according to MALOEUF 1935).

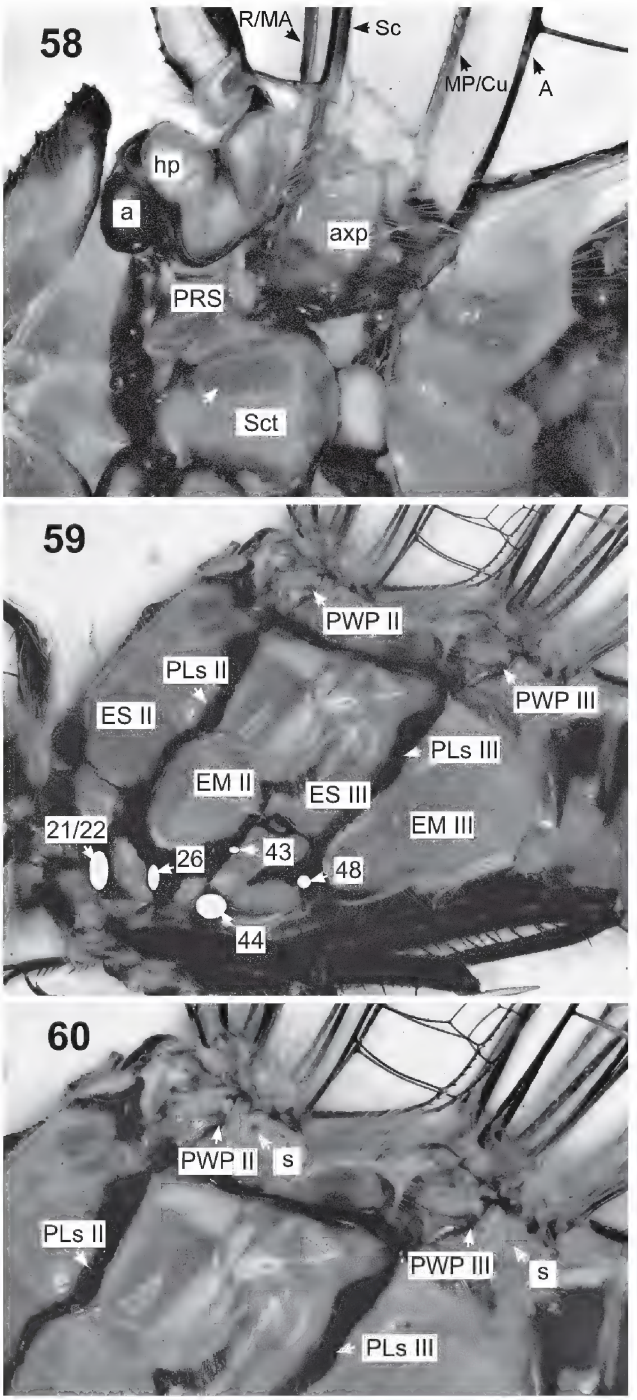
32 (54): The conspicuous pleurosubalar muscle runs from a large dorsal apodeme to the ventral margin of the epimeron. The dorsal apodeme is connected by a tendon to the anterior part of the axillary plate. It is a broad and large muscle in the meso- and also in the metathorax. The muscles 32 and (54) are almost equal in size to the muscles 22 and (44).

33 (55): The pleurosubalar muscle is rather slender and dorsally attached to a small sclerite in the pleural membrane posterior to the PWP, but also to the posteroventral part of the axillary plate by a tendon. Ventrally, it is attached to the epimeron.

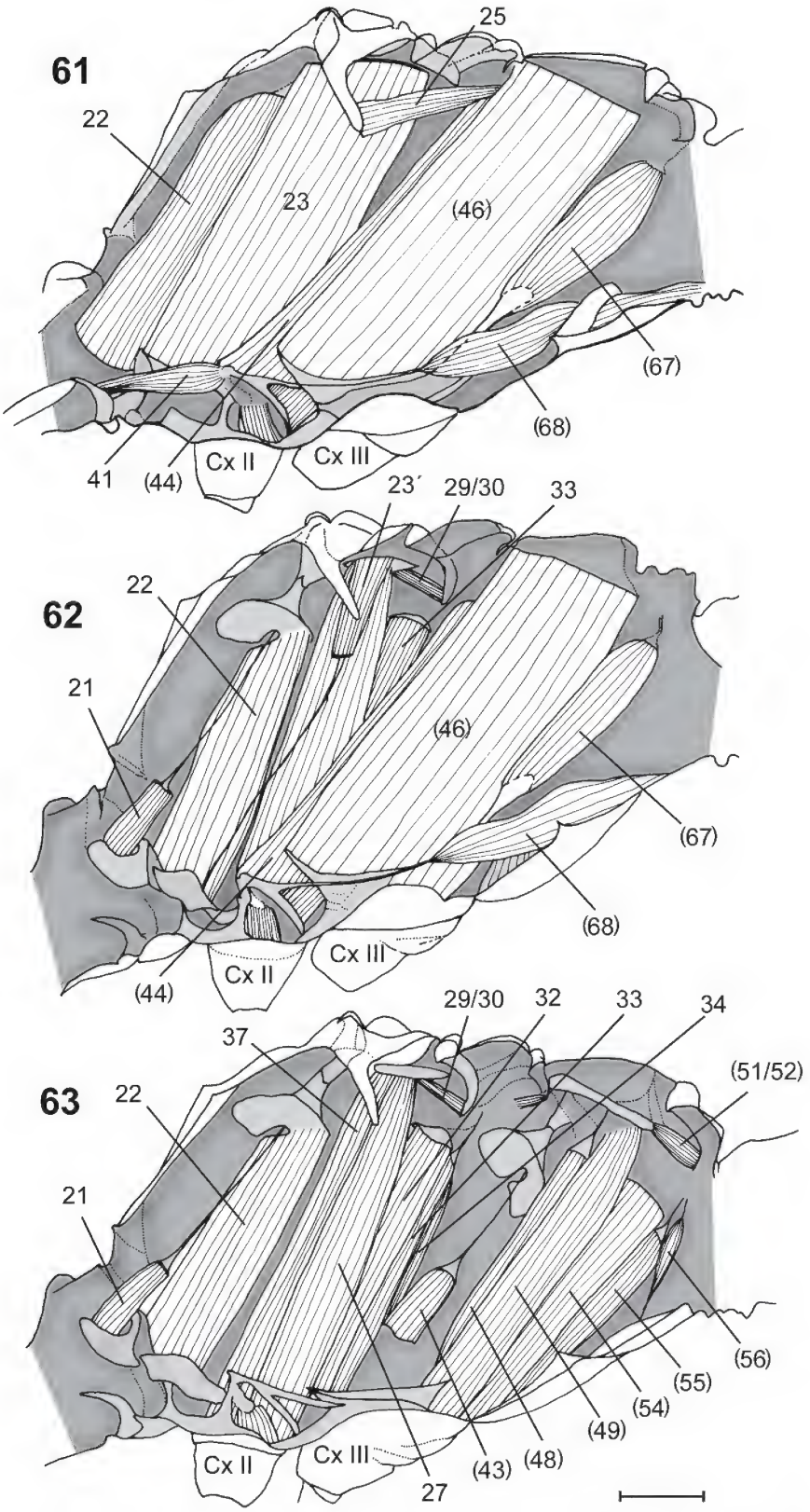
34 (56): Posterior to the muscles 33 and (55) respectively lie the short and slender pleurosubalar muscles 34 and (56) respectively. Muscle 34 is dorsally attached to the small sclerite in the pleural membrane posterior to the PWP. Nevertheless, it is also connected to the posteroventral part of the axillary plate via a tendon. The ventral attachment is on the epimeron near the spiracle. In the metathorax, it is a short muscle that is attached via a tendon dorsally as well as ventrally. The tendon of the muscle 33 and the tendon of the muscle 34 are associated and intersected so that the attachment of the muscle 34 is located anteriorly and the attachment of muscle 33 lies posteriorly. The metathoracic muscles (55, 56) proceed in the same way.

36 (58): The short and flat but robust pleurocoxal muscle runs from the katepisternum (terminology following ASAHINA 1954) to the lateral rim of the coxa.

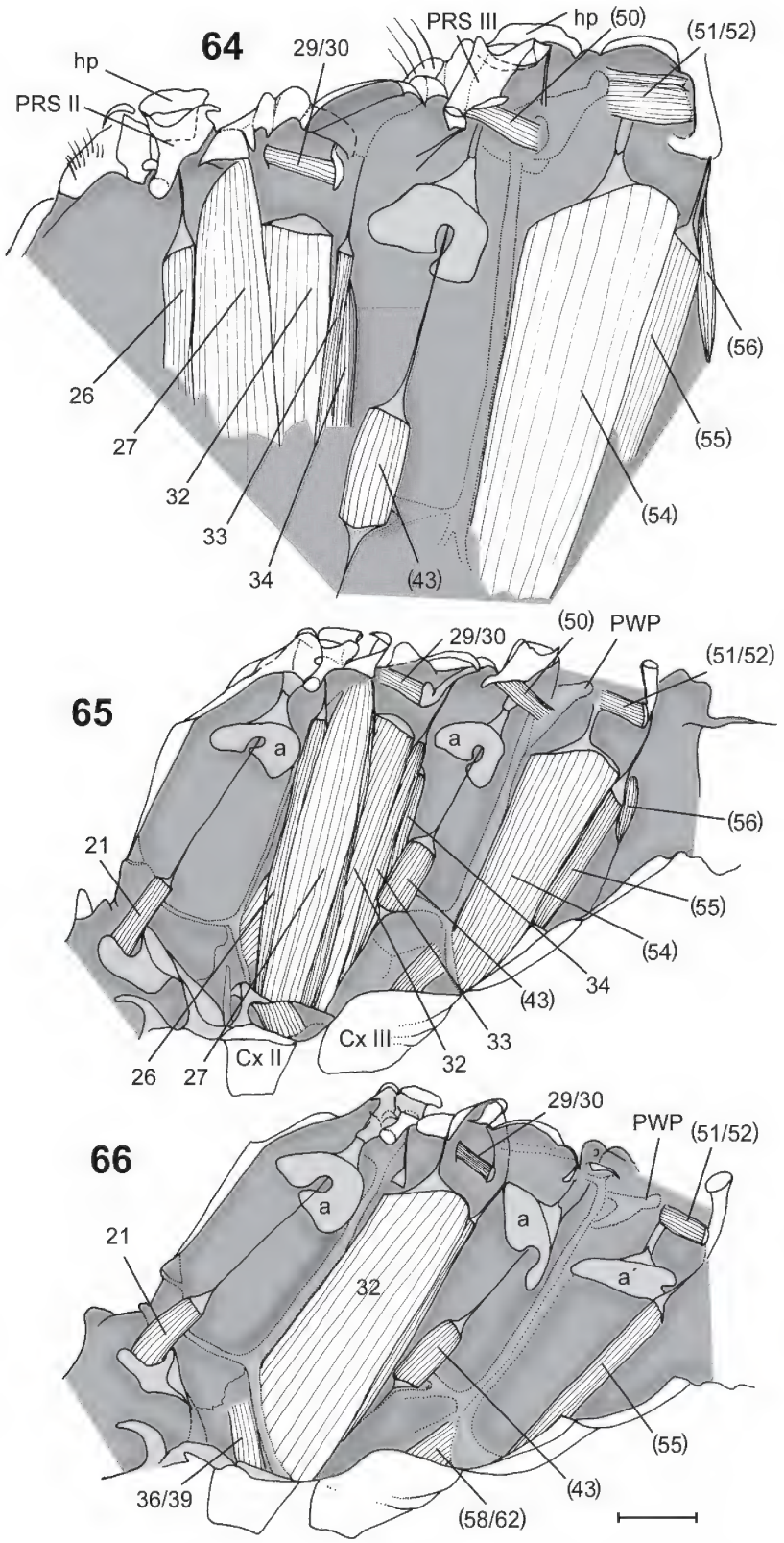
37 (60): The tergocoxal muscle is relatively large and dorsally attached to a tergal sclerite posterior to PRS. Ventrally, the muscle 37 is attached to the anterolateral rim of the coxa. The metathoracic muscle (46) seems to consist of three parts; the first part is the muscle (46), the second is the small muscle (46') and the third part is the muscle 37 (see section 4.3).



Figs. 58–60. *Sympetrum* cf. *striolatum*. – **58**. Mesotergum, dorsal view (head to the left); the arrow marks the apodeme shining through the arced scutal sclerite, which is the dorsal attachment of muscles 23 and 46. **59**. Pterothorax with the ventral attachment points of several muscles, lateral view. **60**. Pterothorax, upper area. – a = regio anterior of hp (following TANNERT 1958); s = dorsal attachments (sclerites) of muscles 33 (55) and 34 (56).



Figs. 61–63. *Sympetrum* cf. *striolatum*, ♂, musculature of the right half of the pterothorax at progressive stages of dissection, starting with median muscles (61) and progressively proceeding to the most lateral muscles (see Fig. 66). – Scale: 1 mm.



Figs. 64–66. *Sympetrum* cf. *striolatum*, ♂, musculature of the right half of the pterothorax at progressive stages of dissection (see legend to Figs. 61–63); Fig. 64 = detail of the upper half. – a = apodeme of muscles 22 and 44; a′ = apodeme of muscle 32. – Scale: 1 mm.

38 (61): The small sternocoxal muscle is stretched between a ventral apodeme (furca 2 following ASAHINA 1954) and the postero-lateral rim of the coxa.

39 (62): The slender pleurotrochanteral muscle 39 is attached to the katepisternum and runs to the trochanter.

40 (63): The pleurotrochanteral muscle stretches between the latero-external side of the furca and the trochanter (following ASAHINA 1954). It is not pictured in Figs. 61–66 because it was hardly visible.

41: The slender and robust longitudinal ventral muscle stretches between the mesofurca and the profurca.

(68): This ventral muscle stretches between the intersegmental sternopleural process (MALOEUF 1935; posterior end of furcal invagination following ASAHINA 1954) and the first abdominal segment. It is a distinct and robust metathoracic muscle. It might be the corresponding muscle to the mesothoracic muscle 41.

3.4 Plecoptera

3.4.1 *Pteronarcys reticulata* (Figs. 67–73) (n = 1)

Measurements (♂)

Total length: 24 mm. – Length of mesothorax: 3.8 mm. – Length of fore wing: 26.5 mm. – Length of metathorax: 4 mm. – Length of hind wing: 22.5 mm.

External morphology of the mesonotum

The prescutum and the prealar bridge are short but distinct (PAB; Fig. 67; metathorax: Figs. 72, 73). The scutum and the scutellum (SL; Fig. 67; metathorax: Figs. 70, 72) are conspicuous in the mesothorax. The median longitudinal suture (MLs; Fig. 67; metathorax: Figs. 70, 72) is distinct from the anterior part of the scutum to the scutellum. A distinct convex area at the lateral part of the scutum serves as a dorsal attachment point for several dorso-ventral muscles. Both the scutellum (SL) and the postnotum are conspicuous elements of the mesothoracic tergum. The tegula (T; Fig. 68; metathorax: Fig. 72) of the fore wing is distinct and densely covered with setae (more than in the metathorax; the apex of the metathoracic tegula is covered with a couple of long setae and some short ones). The indistinct humeral plate (HP, not pictured) lies at the wing base, posterior to the tegula.

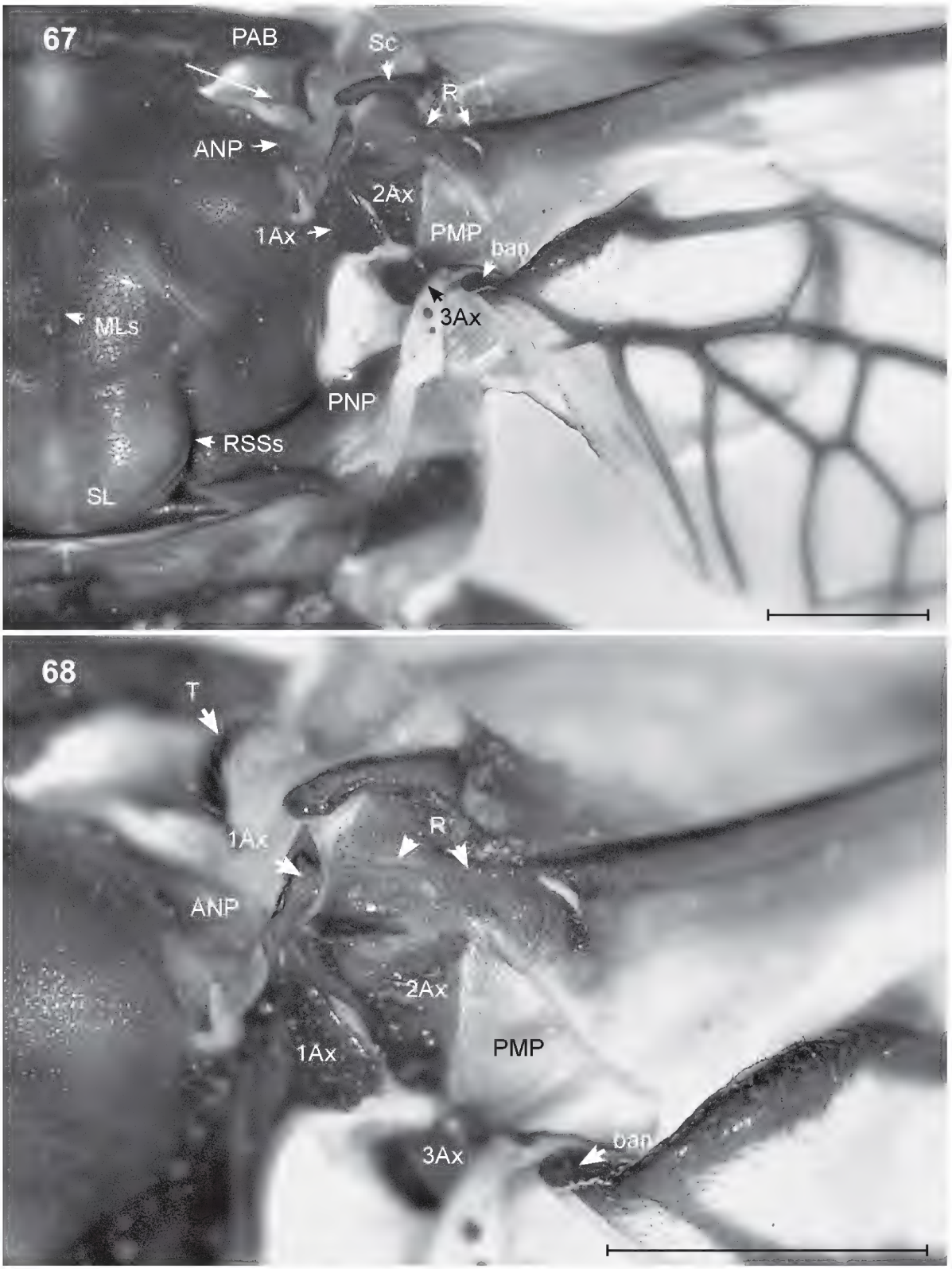
The anterior notal wing process (ANP; Figs. 67, 68) is a concave and clearly demarcated but integral part of the tergum. It is slightly shorter than the ANP of the metathorax (Figs. 70, 72, 73) and approximately four times as long as wide (ANP of the metathorax is approximately six times as long as its width). The median notal wing process (MNP) is weakly developed. The distinct posterior notal wing process (PNP; Figs. 67, 69) articulates with the 3Ax of the wing base. In the metathorax, the anterior part of the PNP (Figs. 70, 72) is detached from the tergum. The axillary cord (AxC) which is sclerotised at its base lies posterior to the PNP.

The wing base is composed of the first, second and third axillary sclerite (1Ax, 2Ax and 3Ax; Figs. 67–69). The 1Ax is subdivided into the anterior head, the middle neck and the posterior body. The entire 1Ax of the mesothorax is rather compact. The head of the 1Ax is almost three times as long as wide and tapered apically (rounded apically in the metathoracic 1Ax). The head of the 1Ax articulates with the subcostal vein (Sc; Fig. 67) but it is also connected to the base of the anterior radial vein (R; Figs. 67, 68). The neck is short and approximately as long as wide. The following body of the 1Ax is almost half as wide as long at its broadest point. It articulates distally with the triangular 2Ax. It is sclerotised only in the dorsal layer of the wing membrane. A muscle is attached to the anterior part of the body of the 1Ax, which runs to the pleurum. In addition to the articulation with the 1Ax proximally, the 2Ax articulates with the proximal median plate (PMP; Figs. 67–69) distally and with the 3Ax posteriorly. The anterior edge of the 2Ax is partly, i.e. over about one half of the edge-length, fused with the base of the anterior radial vein. The distal point of the 2Ax is also fused with the base of the anterior radial vein in the metathorax. The 2Ax is sclerotised both in the dorsal and in the ventral layer of the wing membrane. Seen from dorsally, a distinct sulcus is visible on the proximal part of the 2Ax. It possesses a process on its ventral side, which articulates with the pleural wing process (PWP, not pictured). The 3Ax is distinct and considerably more folded in the mesothorax than it is in the metathorax and is connected to the PNP posteriorly. It is a rather simple sclerite but more robust than in the metathorax and without a pronounced anterior branch. The muscle, which runs to the pleurum (tpm 48) is attached to the proximal cavity of the 3Ax. The posterior part of the 3Ax is connected to the base of the anal veins (A). This base, the basanale (ban; Fig. 68), is conspicuous and sclerotised. Only the proximal one of the two median plates (PMP) is visible.

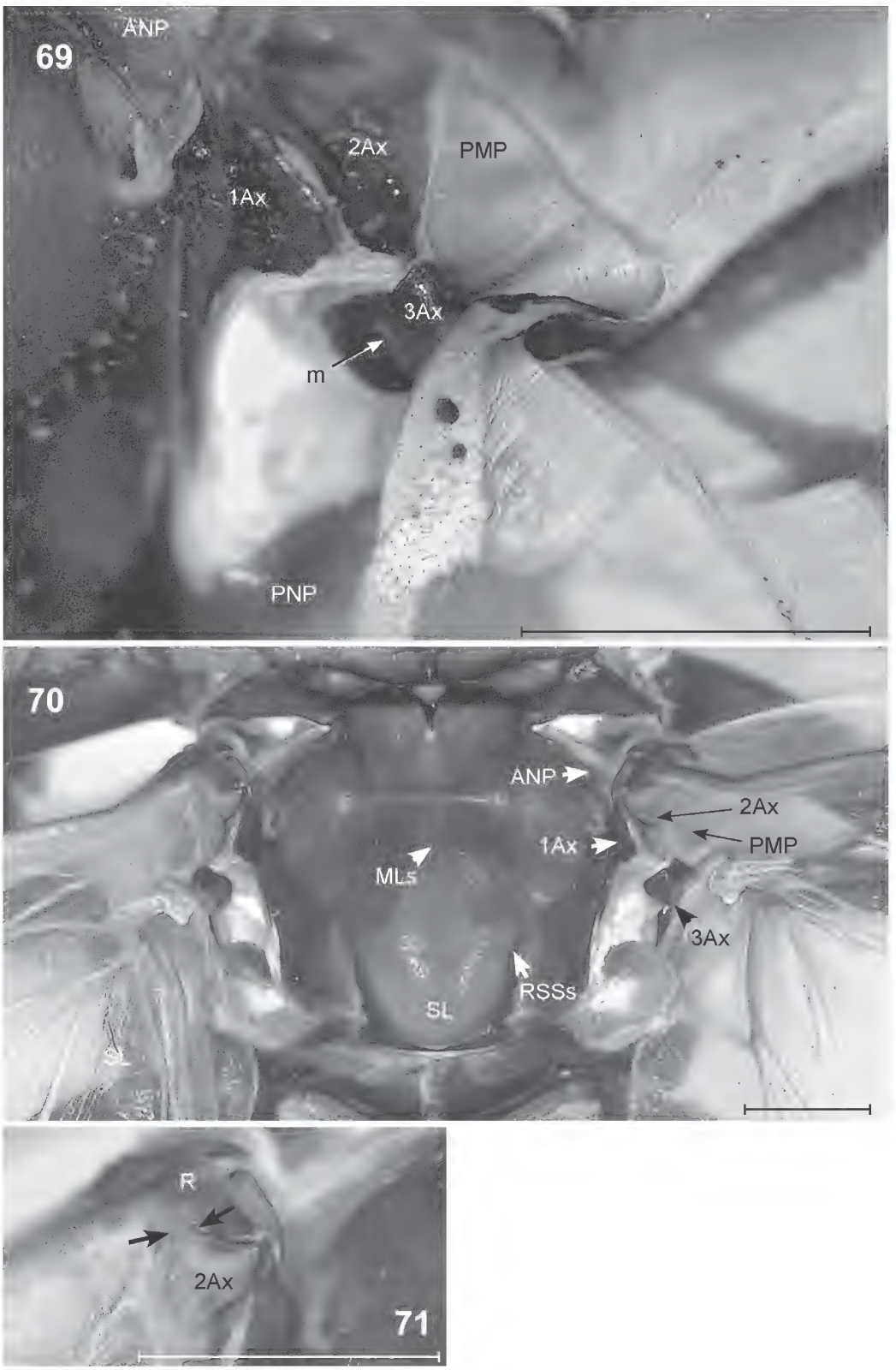
The base of the costal vein, and also the base of the subcostal vein, is distinct. Both are also more conspicuous in the mesothorax than in the metathorax (Figs. 70–73). The anterior radial vein is the most distinct vein in the fore and the hind wing. The base of the anterior radial vein is conspicuously developed. The posterior edge of the base of the radial vein (Fig. 71, R) is partly fused with the 2Ax.

External morphology of the mesopleurum

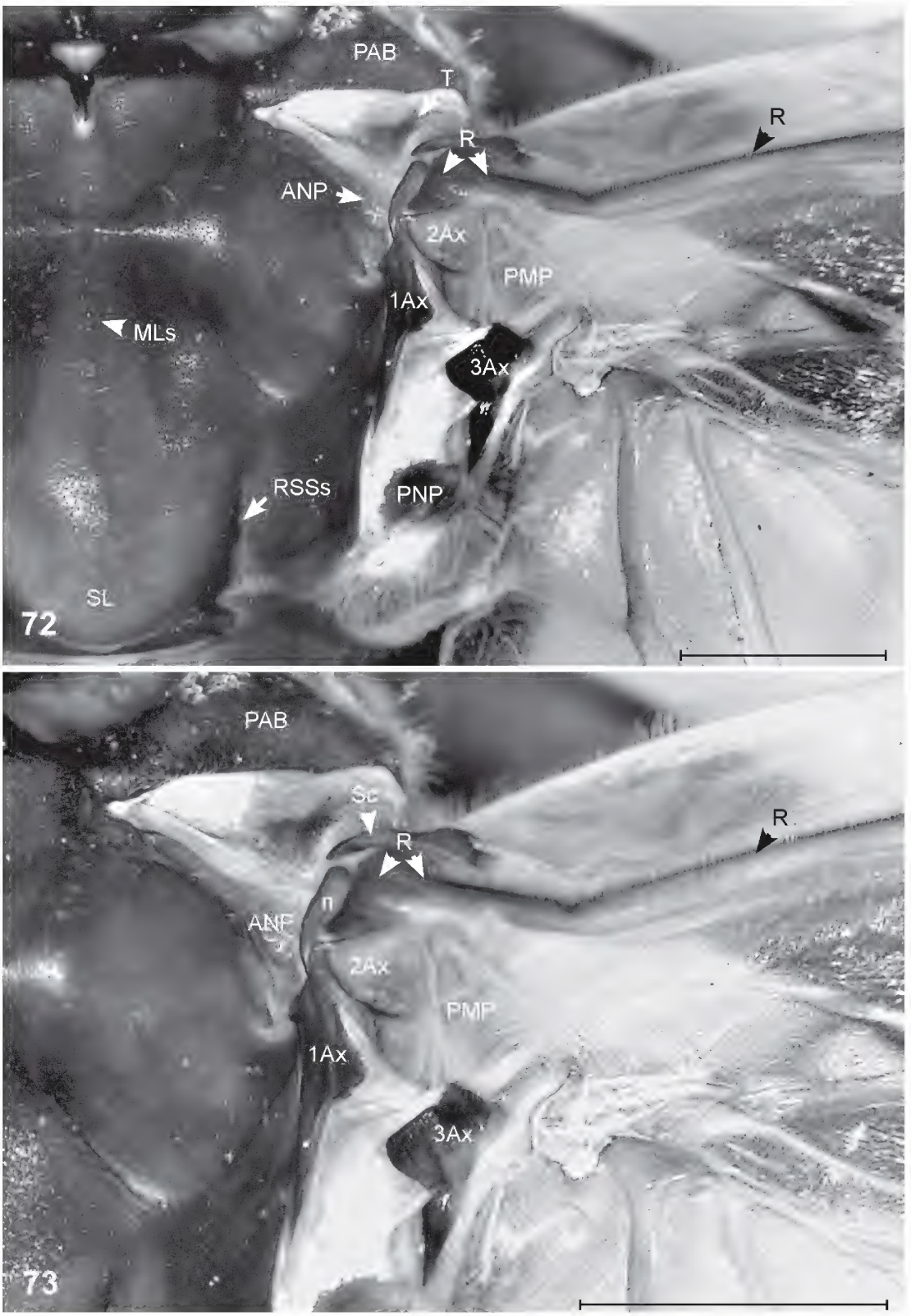
The pleurum (not pictured, compare Fig. 123) is divided into the anterior episternum (ES) and the posterior epimeron (EM) by the pleural suture (PLs), which runs



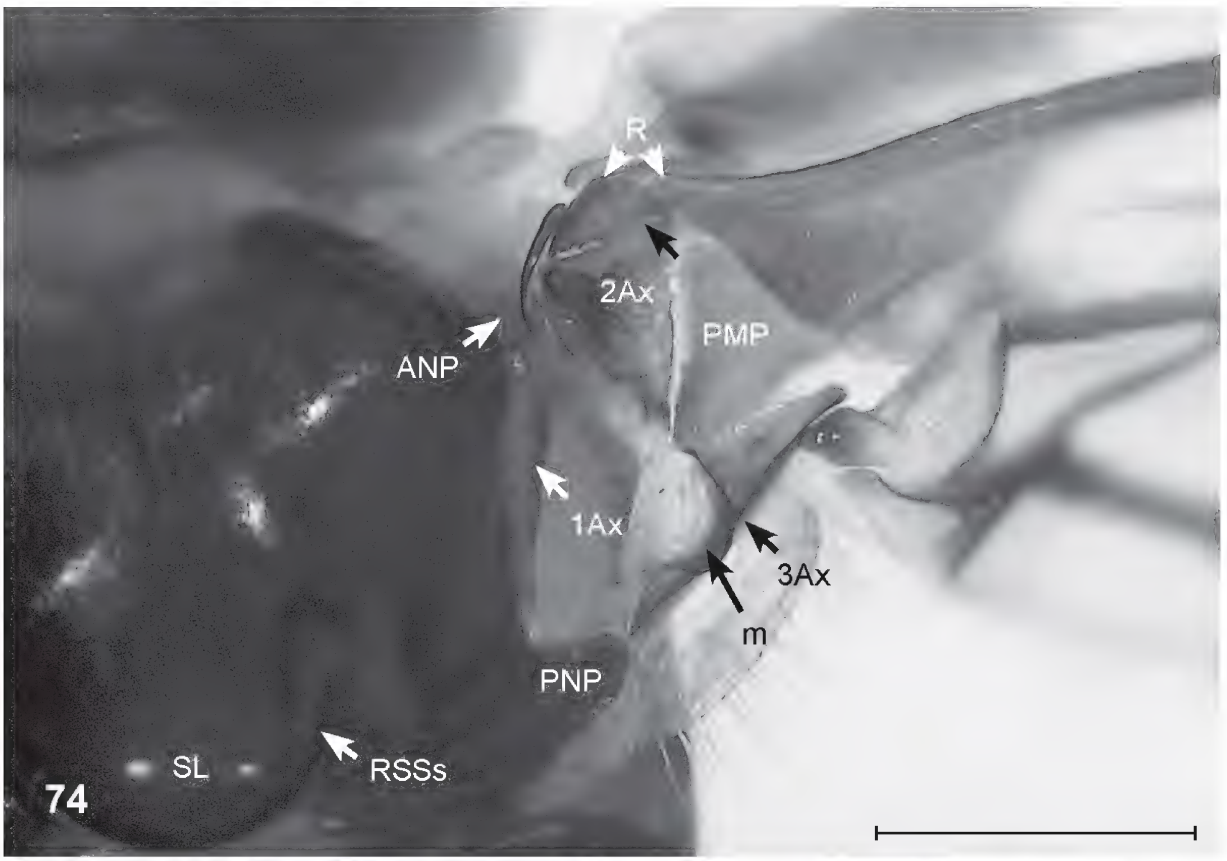
Figs. 67–68. *Pteronarcys reticulata*, right fore wing. – **67**. Wing base; the long arrow marks the position of the subtegula. **68**. Axillary sclerites. – Scales: 1 mm.

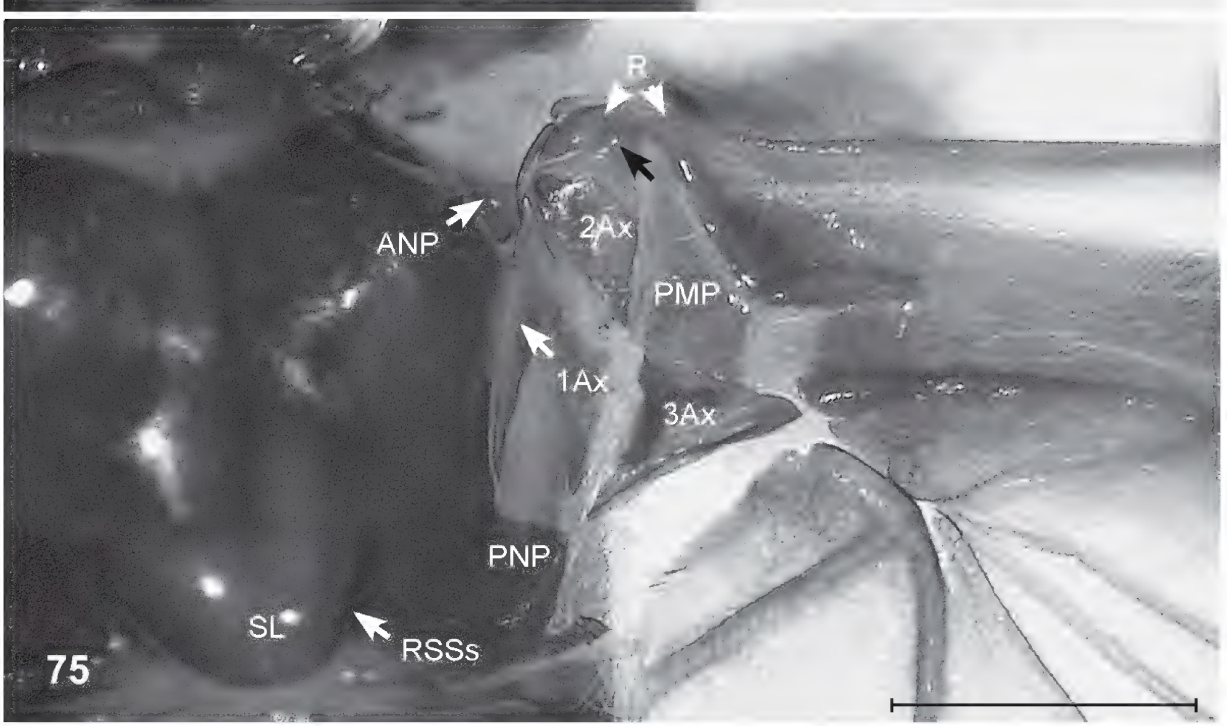


Figs. 69–71. *Pteronarcys reticulata*. – **69**. Detail of the right fore wing; m marks the attachment of the flexor muscle. **70**. Overview of the metanotum and the wing bases. **71**. Detail of the left hind wing base, showing the base of the anterior radial vein (R) and the 2Ax; the arrows mark the fusion of 2Ax and R. – Scales: 1 mm.

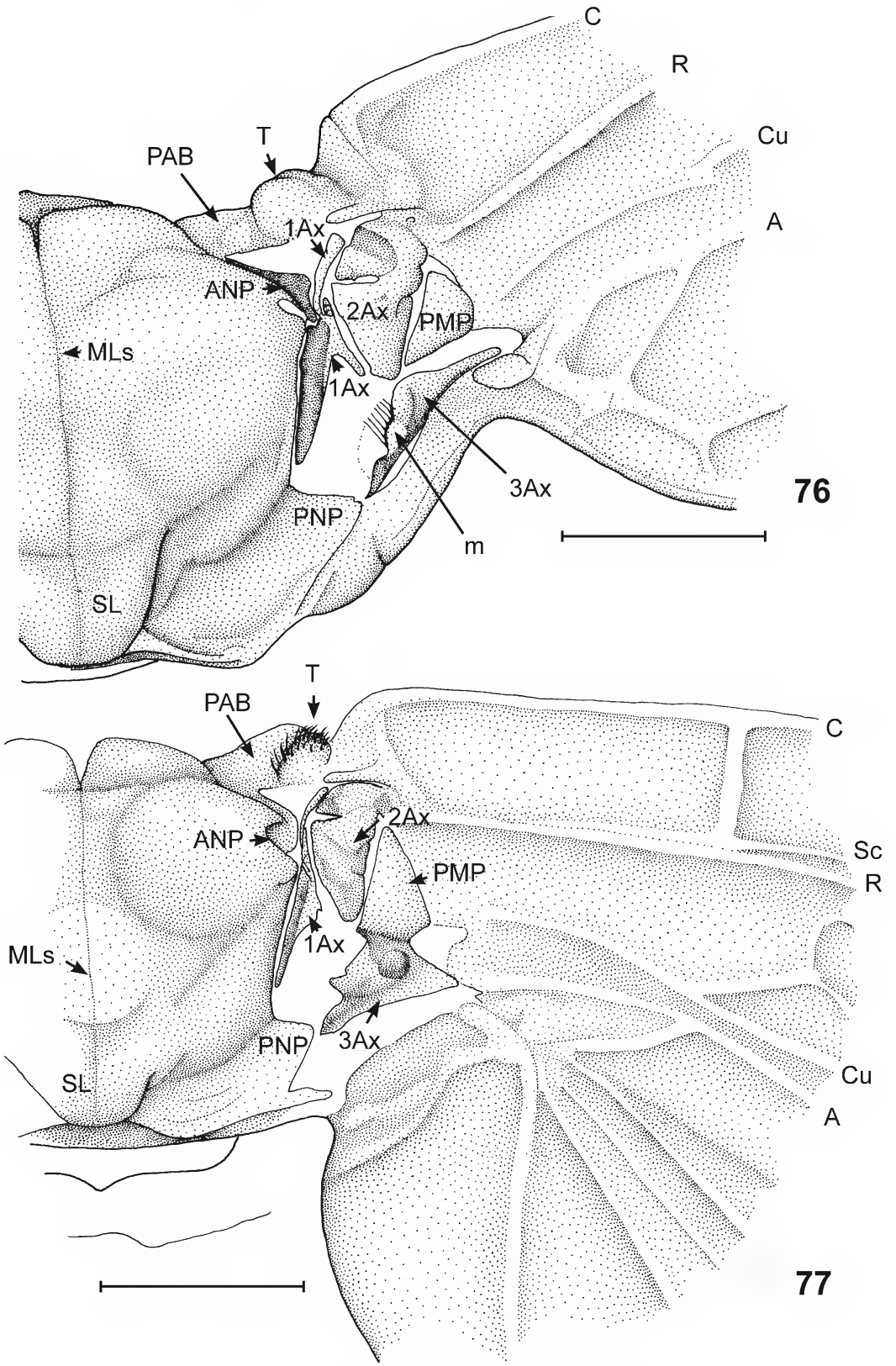


Figs. 72–73. *Pteronarcys reticulata*, right hind wing base; Fig. 73 = detail. – n = neck of 1Ax. – Scales: 1 mm.

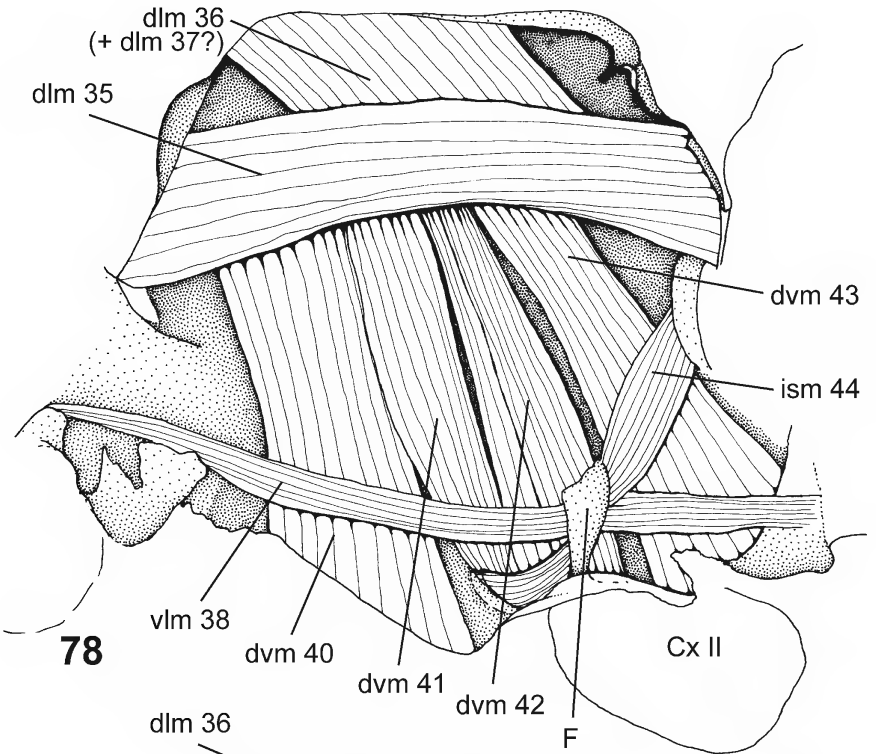


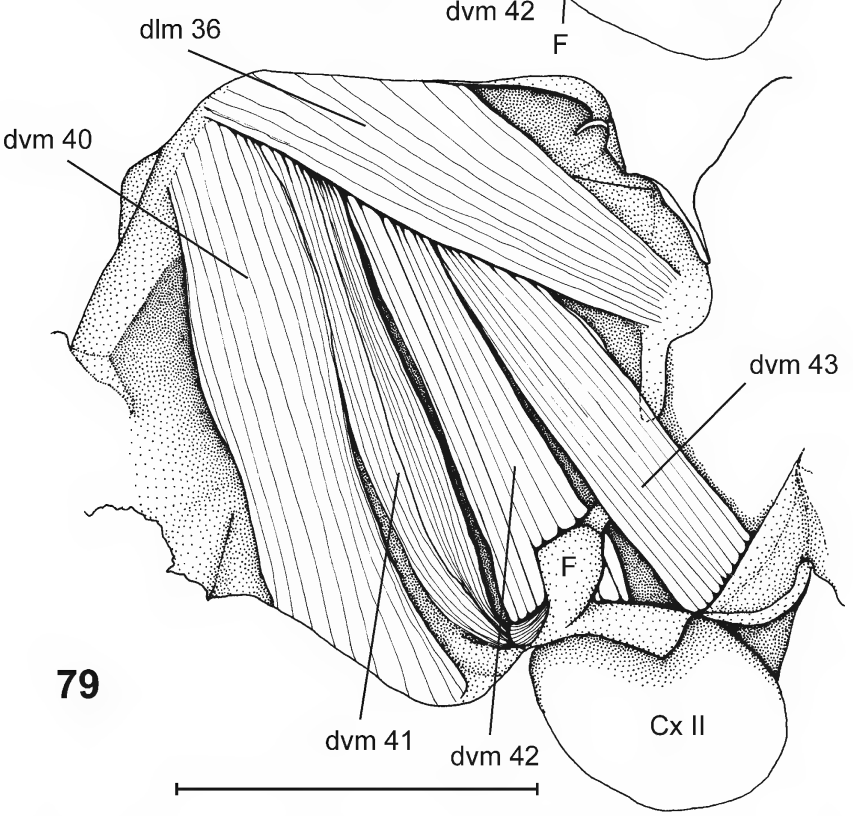


Figs. 74–75. *Brachyptera seticornis*. – **74**. Right fore wing base; m shows the attachment of the flexor muscle of 3Ax; the upper black arrow marks the fusion of 2Ax with the base of the anterior radial vein. **75**. Right hind wing base; the black arrow marks the fusion of 2Ax with the base of the anterior radial vein (R). – Scales: 0.5 mm.

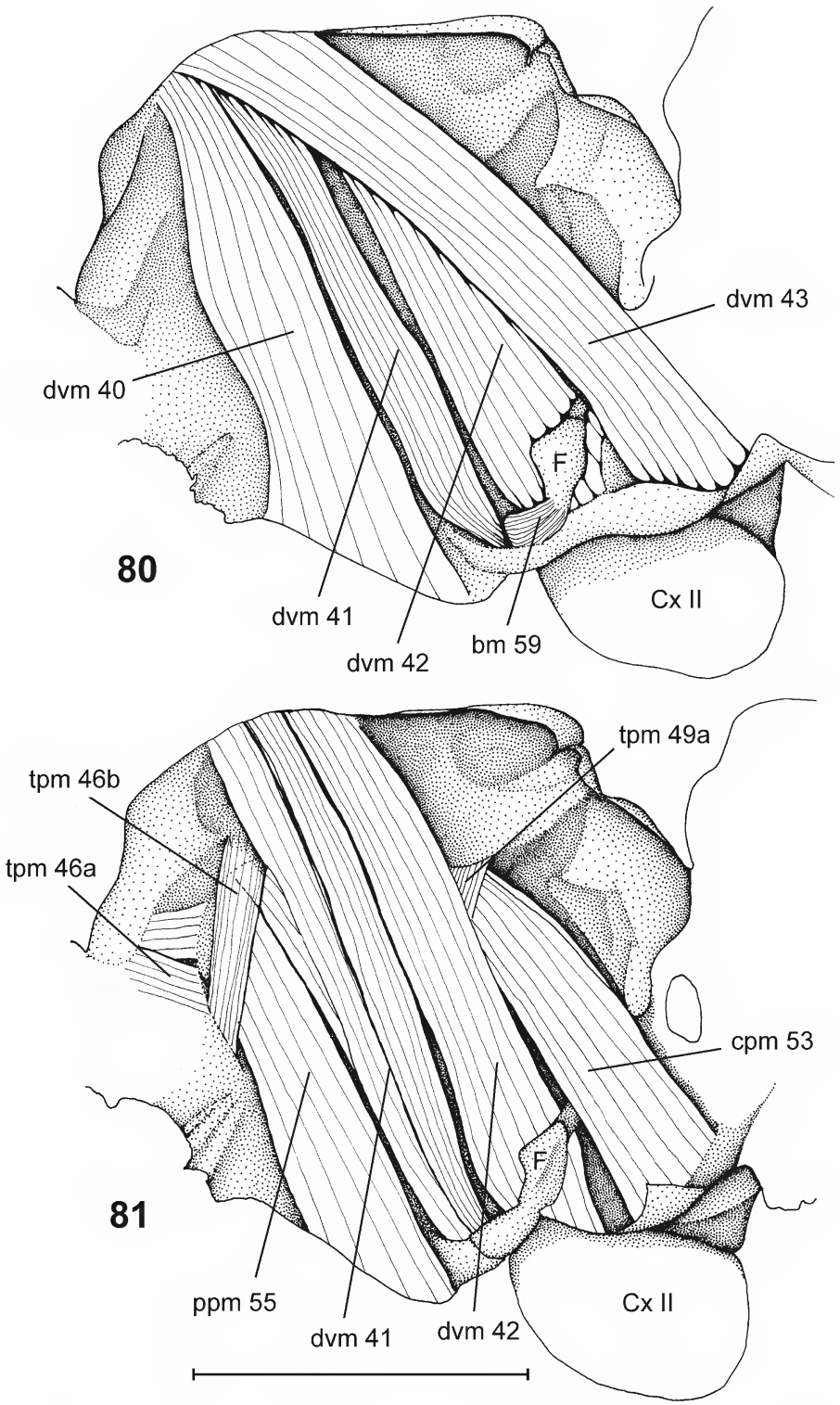


Figs. 76–77. *Brachyptera seticornis.* – **76**. Right fore wing base. **77**. Right hind wing base. – m = attachment of the flexor muscle. – Scales: 0.5 mm.

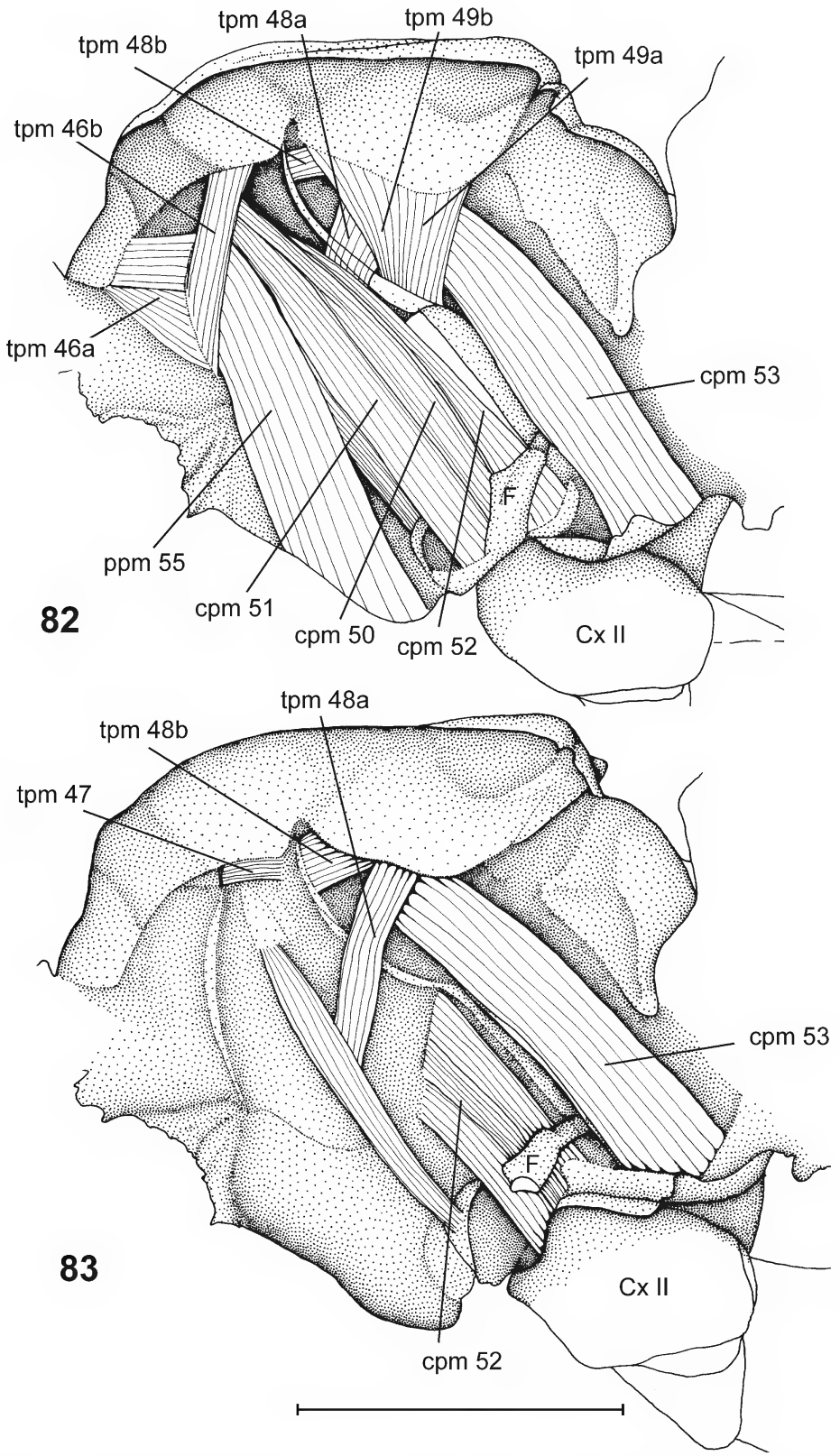




Figs. 78–79. *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (78) and progressively proceeding to the most lateral muscles (see Fig. 83). – Abbreviations of the muscles see section 3.4. – Scales: 1 mm.



Figs. 80–81. *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 78–79). – Scale: 1 mm.



Figs. 82–83. *Brachyptera seticornis*, musculature of the right half of the mesothorax at progressive stages of dissection (see legend to Figs. 78–79). – Scale: 1 mm.

obliquely backwards. The upper part of the pleural suture is less distinct than the conspicuous lower part. The PLs extends dorsally into the pleural wing process (PWP). Anterior to the PWP lies the basalare (BA). It is a prominent part of the pleurum, which is partly detached from the episternum. The basalare is anteriorly connected to the base of the costal vein and to the PWP posteriorly. The subalare is an undifferentiated and longish but distinct sclerite. It is located in the pleural membrane below the wings. The epimeron is not as wide as the episternum.

3.4.2 *Brachyptera seticornis* (Figs. 74–83) (n = 3)

Muscles of the mesothorax (Figs. 78–83)

The musculature in adult specimens is similar in the meso- and metathorax. Therefore, in the following only the mesothorax is described, with the exception of those muscles that are different in each segment. The terminology of musculature follows Wittig (1955) and Zwick (1973).

Dorsal muscles

dlm 35: The Musculus dorsalis longitudinalis is a middle-sized muscle running from the anterior to the middle phragma.

dlm 36: The M. dorsalis obliquus primus is attached to an area stretching from the anterior scutum to the centre of the scutum dorsally and runs to the middle phragma. The dlm 36 is about as large as the dlm 35 but rather flat.

dlm 37: If present, the M. dorsalis obliquus secundus is not clearly separated from the dlm 36.

Dorso-ventral muscles

dvm 40: The M. tergo-praecoxalis (M. tergo-basisternalis sensu Wittig 1955) is a large muscle, which is dorsally attached to the anterior part of the scutum. Ventrally, it is attached to the praecoxa (preepisternite, PES: Fig. 123).

dvm 41: The dorsal point of attachment of the M. tergo-trochantinalis lies just postero-lateral to that of dvm 40 on the scutum. Ventrally, this muscle is attached to the trochantinus. It is a large one, but not as large as the dvm 40.

dvm 42: The M. tergo-endocoxalis, running from the scutum (postero-lateral of dvm 40/41) to the trochanter, is almost as large as the dvm 41.

dvm 43: The dorsal point of attachment of the M. tergo-coxalis posterior lies postero-medial of that of dvm 40. Ventrally, this muscle is attached to the posterior rim of the coxa. The dvm 43 is larger than the dvm 41 and dvm 42.

ism 44: The M. tergo-furcalis is a robust, flat, and broad muscle, which stretches between the antecosta of the metathorax and the furca of the mesothorax.

Pleural muscles

tpm 46b: The M. scuto-apodema episternalis is a flat, broad muscle, which runs from the ANP to the ridge at the anterior part of the episternum. It consists of only a few fibres.

tpm 47: The short and robust M. tergo-crista pleuralis anterior is stretched between the subtegula and the upper part of the episternum next to the PWP.

tpm 48: Two muscles are attached to the 3Ax in *B. seticornis*. The first muscle, the M. pterale [ascellare]-episternalis, is attached to the 3Ax and runs to the episternum slightly ventral to the middle part of the pleural ridge (tpm 48a). It is a flat and broad muscle, which consists of only a few fibres. The second part is attached to the 3Ax (just posterior to the first part) and runs to the upper part of the pleural ridge (below the PWP; tpm 48b) (see discussion, section 4.3.6). It is not as wide as the first part and also consists of only a few fibres. The muscles, tpm 48a and tpm 48b, are wing flexor muscles.

tpm 49: The M. tergo-crista pleuralis posterior is bipartite in *B. seticornis*. The first (anterior) part (tpm 49b) is attached to the anterior part of the body of the 1Ax and to the pleural ridge ventrally. The second (posterior) part (tpm 49a) is stretched between the lateral part of the scutum and the pleural ridge.

cpm 50: The M. basalare-endocoxalis stretches between the antero-dorsal part of the basalare and the trochanter ventrally. The muscles cpm 50 and 51 are similar in dimension to cpm 53

cpm 51: The M. basalare-coxalis is dorsally attached to the basalare and ventrally to the anterior rim of the coxa.

cpm 52: The M. episterno-coxalis stretches between the episternum and the anterior rim of the coxa. The dorsal point of attachment lies postero-ventral to cpm 50 and cpm 51.

cpm 53: The wide M. subalare-coxalis is attached to the subalare and runs to the posterior part of the coxa, the meron.

ppm 55: The M. episterno-praecoxalis is a robust muscle, which stretches between the upper part of the episternum (anterior to the BA) and the ventral part of the episternum.

ppm 56: The M. pleuralis is a flat muscle running from the posterior subalare (terminology following Zwick 1973) to the epimeron and consists of only a few fibres.

bm 59: The short and flat M. furca-coxalis anterior stretches between the furca and the antero-lateral rim of the coxa.

zm 61: The short but distinct and robust M. furca-crista pleuralis connects the furca with the pleural arm.

4 Discussion

4.1 General Remarks

There is generally no doubt on the monophyly of Neoptera. In contrast, the sister group relationships of the three basal clades of Pterygota (Ephemeroptera, Odonata and Neoptera) remain controversial. While there is general agreement on the composition of the wing base sclerites in the ground plan of Neoptera, their homology to the wing base sclerites in Ephemeroptera and Odonata has remained unresolved. This is mainly due to the fact that the conditions in the Ephemeroptera and Odonata seem to be highly modified, since both taxa are specialised in this respect. However, it will only be possible to deduce the ground plan of the pterygote wing base when the homology of these elements is clarified.

4.2 The wing base elements

The following chapters provide a short summary of the wing base morphology of Ephemeroptera, Odonata and Neoptera and also of earlier assumptions to the homology of wing base sclerites and their musculature before the interpretation is given.

4.2.1 The wing base of Neoptera (Figs. 67, 70–72, 84, 85)

In the ground plan of Neoptera the wing base is composed of the tergal anterior notal wing process (ANP), the median notal wing process (MNP), and the posterior notal wing process (PNP). Furthermore, there are three axillary sclerites (1Ax, 2Ax, 3Ax), the proximal median plate (PMP) and the distal median plate (DMP) in the wing base of Neoptera (Brodsky 1994, Snodgrass 1935). The PMP as well as the DMP are sclerotised in both the dorsal and ventral layer of the wing membrane, which alludes to a wing vein origin.

The first axillary sclerite (1Ax) articulates with the ANP and, if present, also with the MNP proximally and with the second axillary sclerite (2Ax) distally. The 1Ax is sclerotised only in the dorsal layer of the wing membrane, which alludes to its tergal origin. It is directed approximately parallel to the longitudinal axis of the insect body. Furthermore, it is divided into the anterior head and neck and the posterior body. The head articulates with the subcostal vein.

The 2Ax articulates proximally with 1Ax, distally with the proximal median plate (PMP), and posteriorly with the 3Ax. The anterior part of the 2Ax is also connected to the base of the anterior radial vein. The 2Ax is sclerotised both in the dorsal and ventral layer of the wing membrane. A proximo-ventral process of the 2Ax articulates with the pleural wing process (PWP).

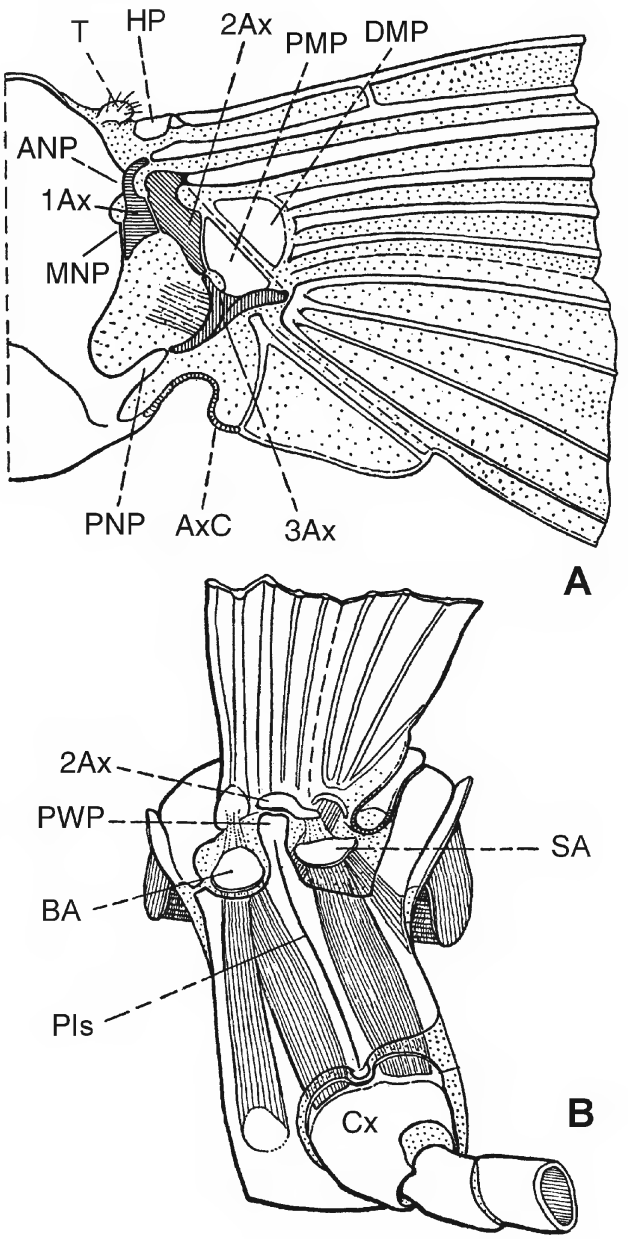


Fig. 84. Schematic representation of the neopterous wing base (modified after Snodgrass 1935: figs. 122, 129). – **A**. Dorsal view. **B**. Lateral view.

The 3Ax articulates, in addition to the articulation with the 2Ax and the PMP, also with the posterior notal wing process (PNP). It is also connected to the anal veins and the jugal veins of the wing. Furthermore, it is sclerotised in both the dorsal and ventral layer of the wing membrane. The 3Ax is orientated acute-angled (about 60°) or

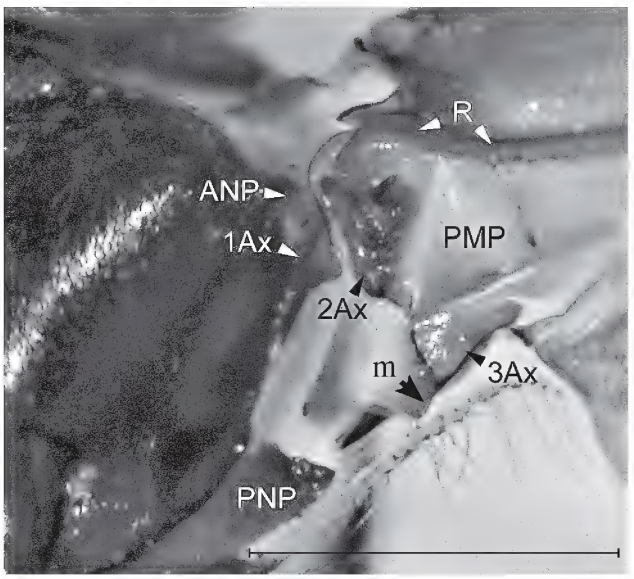


Fig. 85. *Leuctra hippopus*, right fore wing base. – m = attachment of the flexor muscle of 3Ax. – Scale: 0.5 mm.

approximately perpendicular to the longitudinal insect body axis (Brodsky 1994, Snodgrass 1935).

Further wing base elements in the ground plan of Neoptera are the basalare (BA) anterior to the pleural wing process (PWP) and the subalare (SA) posterior to the PWP (Brodsky 1994, Hörnschemeyer 2002, Snodgrass 1935).

In previous contributions it is assumed that in the ground plan of Neoptera only the 3Ax serves as dorsal attachment of a muscle running to the pleurum (e. g. Snodgrass 1935). Both the first and third axillary sclerite are provided with such a muscle. A wide but flat muscle (Fig. 125) inserts on the proximal part of the 1Ax and proceeds to the pleural ridge in Plecoptera (Willkommen & Hörnschemeyer 2007). The proximal part of the 3Ax is the dorsal attachment of a flat muscle running to the episternum (t-p 13 sensu Matsuda 1970). This muscle together with the wing base morphology (e. g. axillary fold- and flexion-lines, shape of axillary sclerites) enables the Neoptera to fold their wings horizontally over the abdomen. In several Neoptera a second muscle occurs, which is stretched between the 3Ax and the upper part of the pleural ridge (t-p 14). According to Brodsky (1994) both muscles are present in insects which fold their wings over the back in a roof-like position (with exception of Psocoptera) and are also present in Diptera (which do not fold their wings in such manner), but insects, which fold their wings flat have only one of the muscles attached to the 3Ax. Nevertheless, Plecoptera have both muscles attached to the 3Ax. This suggests that the presence of two muscles attached to the 3Ax is most likely a ground plan character of Neoptera. Moreover, both the ANP and the PNP are each provided with a muscle that proceeds to the pleurum.

In addition, there are flight muscles associated with the basalare and the subalare: at least two basalar muscles (basalar-trochanteral and basalar-coxal muscle) and one or two subalar muscles (subalar-coxal and subalar-pleural muscle) are present in the Neoptera.

4.2.2 The wing base of Odonata (Fig. 58)

The morphology of pterothorax, wing base, and venation of Odonata were examined by different authors (e. g. Asahina 1954; Bechly 1996; Hatch 1966; Pfau 1986, 1991; Riek & Kukalová-Peck 1984; Tannert 1958). The two plates in the wing base of Odonata are termed differently in these publications (Tab. 2). The anterior plate is either the humeral plate (sensu Snodgrass 1935 and Asahina 1954) or costal plate (sensu Tannert 1958). The posterior plate is termed axillary plate by Snodgrass (1935) and Asahina (1954) or radio-analis plate by Tannert (1958).

The wing base is articulated with the thoracic tergites by the anterior humeral plate and the posterior axillary plate. The humeral plate is sclerotised only dorsally and articulates with the anterior pleural process. The humeral plate of Odonata is supposed to be a product of a secondary fusion of the humeral plate of Neoptera with the base of the costal vein (Tannert 1958). Snodgrass (1935), however, does not assume such a secondary fusion but rather an enlargement of the humeral plate alone. Based on his morphological data Asahina (1954) supposed that a part of the basalare is fused with the humeral plate and that a part of the subalare is fused with the axillary plate of the wing base.

Brodsky (1994) assumed – without arguments – that only t 14 of Odonata can be homologised to the respective muscles of other Pterygota and that the humeral plate contains at least a part of the basalare.

The radial and the anterior medial veins originate from the dorsal part of the axillary plate. The sector of the medial vein (except the anterior medial vein), the cubitus and the analis originate from the ventral part of the axillary plate (Tannert 1958). The posterior pleural wing process of Odonata articulates with the anterior part of the axillary plate. There are two short muscles stretched between the postero-internal side of the axillary plate and the membrane just posterior to the pleural wing process (Asahina 1954).

Tab. 2. Terminology of the wing base sclerites of Odonata.

Position	Snodgrass 1935, Asahina 1954	Tannert 1958
anterior plate	humeral plate	costal plate
posterior plate	axillary plate	radio-analis plate

4.2.3 The wing base of Ephemeroptera (Figs. 2, 3, 27–29, 40–42, 94, 95)

The most conspicuous element in the wing base of Ephemeroptera is the basal plate (BP). Its proximal part is flat and articulates with the pleural wing process (PWP). Furthermore, three sclerites are present lying proximal to the BP. The first free wing base sclerite (s1) articulates proximally with the anterior notal wing process (ANP) and distally with the second wing base sclerite (s2). It is sclerotised only in the dorsal layer of the wing membrane and there is no muscle attached to it. The second sclerite (s2) is proximally connected to the s1, distally to the BP and posteriorly to the s3. It is sclerotised only in the dorsal layer of the wing membrane and has a proximal process, which is bent inwards. In basal Ephemeroptera two muscles are attached to s2. The first muscle is running to the pleurum and the second one is attached to the furca. The third wing base sclerite is tightly associated with the BP and is sclerotised in both dorsal and ventral layer of the wing membrane. Posteriorly it articulates with the posterior notal wing process (PNP). The s3 is provided with a short muscle running to the pleurum next to the PWP.

4.2.4 Current hypotheses on the homology of wing base sclerites (Figs. 86–88)

Hitherto several authors (Bekker 1954; Brodsky 1970, 1974, 1994; Grandi 1947; Kluge 1994, 2004; Kukalová-Peck 1974a, 1974b, 1978, 1983, 1985, 1987; Kukalová-Peck & Brauckmann 1990; Matsuda 1956, 1970; Tsui & Peters 1972, Willkommen & Hörnschemeyer 2007) proposed different hypotheses for the homology of wing base sclerites and the associated muscles between the basal pterygote taxa.

Grandi (1947) examined *Ephemerella* sp. (Ephemerellidae), *Ephemera* sp. (Ephemeridae), *Ecdyonurus* sp. (Heptageniidae), *Choroterpes* sp., *Habrophlebia* sp. (Leptophlebiidae), several Baetidae, *Oligoneuriella* sp. (Oligoneuriidae) and *Caenis* sp. (Caenidae). She assumed that the wing base sclerites of Ephemeroptera are pseudopteralia without homology to the wing base sclerites of other Pterygota. The three pseudopteralia are the pseudopterale prossimale (primo; s1), the pseudopterale mediale (secondo; s2) and the pseudopterale distale (terzo; proximal base of the basal plate).

Kluge (1994: 557, 2004) suggested that there is no agreement on homologisation of these sclerites with the axillary sclerites of Neoptera. Therefore, he termed the first sclerite (s1) of the ephemeropteran wing base anterior axillary sclerite (term used by Bekker 1954: aAx), the second sclerite (s2) was named the middle axillary sclerite, and the third sclerite (s3) was termed the posterior articulatory process.

Kukalová-Peck (1983, 1987, 1998) assumed that the wing articulation, namely the axillary sclerites, originated from an additional part of the pleura, which articulated above the subcoxa. In her interpretation the wing base of the pterygote ground plan consists of 32 wing base sclerites, which are arranged in eight rows. The sclerites are termed the proxalaria, the axalaria, the fulcalaria and the basivenales (from proximal to distal). She assumed that the proxalaria originated from the epicoxa and the axalaria and the fulcalaria probably originated from the wing membrane.

Matsuda (1956) examined the thorax of *Siphlonurus columbianus* (Siphlonuridae) and ascertained that the ordinary three axillary sclerites are clearly recognisable. Each sclerite maintains the typical topographical position compared to the other axillary sclerites and to the anterior and posterior notal wing process. He further (l. c., p. 96) mentioned that Grandi (1947) "failed to recognize the presence of the third axillary sclerite in a series of species she examined". The sclerite homologous to the 3Ax of Neoptera should be the additional sclerite (s5) in the wing base of several mayflies, e. g. *Siphlonurus columbianus*, *S. aestivalis* (Siphlonuridae) and *Rhithrogena semicolorata* (Heptageniidae) and the absence of the s5 would be secondary. Furthermore, he homologised the s1 and the s2 of the ephemeropteran wing base with the 1Ax and the 2Ax of the neopteran wing base (Fig. 86). The muscle that is attached to the posterior part of the second free sclerite (s2) and running to the pleurum is homologised by him with the muscle that inserts on the 3Ax in Neoptera. The axillar-furcal muscle (Ax.Fm sensu Kluge 1994) as well as the loss of the relationship between the wing base sclerites and the wing veins is according to this author peculiar to the mayflies.

Tsui & Peters (1972) examined the thorax of selected genera of the Leptophlebiidae. In five genera they found two axillary sclerites and only in *Aprionyx* three. The homology that is proposed for the sclerites s1 (1Ax) and s2 (2Ax) is the same that is suggested by Matsuda (1956). The third axillary sclerite in *Aprionyx* (see above) is mentioned only in the text (equivalent to s5) but not in their drawings. The authors described a muscle running from the subalare to the median plate (equivalent to basal plate, BP). "The similar function of this muscle between the Ephemeroptera and other pterygotes is considered by Matsuda (pers. comm.) as convergent evolution." (Tsui & Peters 1972: 340).

Bekker (1954) assumed that the movements of the wings are regulated via five sclerites. Three of them are located between the tergum and the wing namely the anterior axillary sclerite (aAx – equivalent to s1), the first axillary sclerite (1Ax – equivalent to s2) and the fourth axillary sclerite (4Ax). There are two additional sclerites, the second axillary sclerite (2Ax – equivalent to the whole BP) and the third axillary sclerite (3Ax – equivalent to s3), that

correspond to the 2Ax and the 3Ax of Neoptera. He described a bipartite muscle with one part running from the 3Ax to the pleurum and a second part that is attached to the 2Ax (equivalent to BP).

Two publications of Brodsky (1970, 1974) presented contradictory conclusions (Figs. 87, 88). According to Brodsky (1970) the first wing base sclerite (s1) of Ephemeroptera is homologous with the ANP of Neoptera, s2 is assumed as homologous to the first axillary (1Ax of Neoptera) and the homologous part to the 2Ax of Neoptera is fused with the basal plate in Ephemeroptera. The third wing base sclerite (s3) should be homologous with the 3Ax of Neoptera. Given the hypothesis of Brodsky (1974) the s1 of Ephemeroptera is homologous with the 1Ax of Neoptera, the s2 is assumed as homologous with the 2Ax and the s3 should be the homologous structure to the 3Ax of Neoptera. The additional sclerite (s5) of the ephemeropteran wing base is assumed to be a median notal wing process (MNP), which is not homologous with the MNP of Neoptera.

4.2.5 Homology of the wing base sclerites and axillary muscles (Figs. 89, 91)

Grandi (1947) assumed that the wing base elements of Ephemeroptera are not homologous with that of other Pterygota. This implies that the wings and wing base sclerites must have developed twice and independent from the other Pterygota. This assumption is, however, rather unlikely. Kluge (1994, 2004) gives no interpretation of wing base homology.

First free wing base sclerite – s1

The first free wing base sclerite (s1; Figs. 3, 29, 41, 94–95, 107) in the mayfly wing base is usually characterised as follows: A narrow, triangular sclerite, sclerotised only in the dorsal layer of the wing membrane, articulates proximally with the anterior part of the notum and distally with s2; in relation to the tergum it is orientated obliquely to the longitudinal body axis. It is not directly associated with any wing vein. No muscle is attached to it, except in *H. confusa* (Leptophlebiidae) where a slender and indistinct tendon diverges from the main part of BA.Cm and is attached to the s1 (own observation). In the examined Baetidae and also in Oligoneuriidae (*Elassoneuria* sp., *Oligoneuriella rhenana*) the s1 is rather large in relation to the body size, in *Habroleptoides confusa* (Leptophlebiidae) and *Caenis rivulorum* (Caenidae) it is inconspicuous, in *H. confusa* it is not distinctly differentiated, and in *C. rivulorum* (Baetidae) it is narrow (own observations).

Matsuda (1956) assumed that the s1 is the first axillary sclerite because a muscle is attached to this sclerite and to the coxal process ventrally. Furthermore, he wrote that the basalar-coxal muscle is absent in *Siphlonurus columbianus*, though Maki (1938) described this muscle. The two mentioned muscles (axillary-coxal and basalar-coxal muscle) are, however, one and the same muscle in real terms. The problem of the different interpretations of this muscle is the dorsal attachment. At first sight, the muscle seems to be attached to the s1, but on closer examination one can see that it is attached to a dorsal sclerite directly anterior to the s1 (Fig. 11) (exception *Habroleptoides confusa*, see above).

The first axillary sclerite (1Ax) in Plecoptera is provided with a muscle running to the pleurum (Fig. 125). Furthermore, between the first and the second axillary sclerite runs a convex axillary flexion-line (Wootton 1979). Neither the first nor the second fact applies to the s1 in the ephemeropteran wing base.

Brodsky (1970) assumed that the s1 (sclerite A in his paper) is likely to be the ANP. He examined the final instar nymph of the mayfly because it "presents a clearer picture". According to him, the axillary apparatus is represented by five elements short before the moult to the subimago, and the structure of the axillary apparatus of the most specialised forms (Caenidae) suggests that the s1 is homologous with the anterior notal wing process. Probably, this is the right interpretation because the ANP of the Plecoptera (Figs. 67–70, 72, 73) lies in the same position as the s1 in Ephemeroptera. It is a concave and clearly demarcated but integral part of the stonefly tergum (Willkommen & Hörnschemeyer 2007). In contrast to Brodsky (1970), Brodsky (1974) assumes that the s1 is the first axillary sclerite. Consequently, he ascertains that the lack of a connection between the 1Ax and the subcostal vein is specific to mayflies. But the latter is irrelevant if one assumes that s2 is homologous with 1Ax of Neoptera (see below).

Thus, the orientation, sclerotisation and the (lacking) connection to the wing veins indicate that the s1 is a detached part of the ANP rather than the homologous part to the first axillary sclerite (1Ax) of Neoptera.

Second free wing base sclerite – s2

The 1Ax of Neoptera is characterised by the following: It is sclerotised only in the dorsal layer of the wing membrane, is connected to Sc and provided with a muscle running to the pleurum, and is characterised by a convex axillary flexion-line lying distally.

The second free wing base sclerite (s2; Figs. 3, 41, 94–95, 107) of the ephemeropteran wing base shows characteristics that are also known from the 1Ax of the Neoptera: It is orientated approximately parallel to the longitudinal body axis, it is anteriorly connected to the subcostal vein, it is distally also connected to the 2Ax and the 3Ax (see below). Furthermore, in *Siphlonurus aestivalis*, a basal mayfly, the s2 is provided with two muscles (Ax.PmI, Ax.Fm), which is a plesiomorphic condition following Matsuda (1970). The Ax.PmI is present only in

comparatively basal mayflies, besides *Siphlonurus aestivalis* (own observation) also in *Parameletus chelifer*, *Ametropus eatoni*, and *Metretopus norvegicus* (according to Brodsky 1974), and *Siphlonurus columbianus* (according to Matsuda 1956). Ax.Fm is present in most of the examined mayflies and is probably homologous with the muscle 45 of *Lepisma saccharina* (Zygentoma: Lepismatidae) (Matsuda 1970).

A muscle running from the 1Ax to the pleural ridge is also present in Plecoptera (Fig. 125, tpm 49b). In difference to Ephemeroptera this muscle inserts nearly on the whole length of the body of the first axillary sclerite (1Ax) in Plecoptera whereas in *S. aestivalis* (Siphlonuridae) it arises only from one point of the axillary sclerite.

Matsuda (1956) assumed that the muscle Ax.PmI (sensu Kluge 2004) shows a striking similarity to the wing flexor muscle in other pterygote insects, which usually inserts on the third axillary sclerite. However, its dorsoventral course, its insertion not on the posterior but on the middle part of the wing base, precludes a function as a wing flexor. Matsuda's interpretation resulted from the fact that he neither recognised the separate sclerite that is directly associated with the basal plate (BP) of the wing (lying in the same position as the 3Ax in Neoptera, see below) nor the muscle that is attached to it.

Matsuda (1956) described a muscle running from the posterior notal process (PNP) to the base of the median plate (basal plate, BP). This muscle is present in nearly all examined Ephemeroptera but it is attached to the third wing base sclerite (s3) running to the anterior part of the subalare (or the pleurum). Sometimes this muscle is bipartite and the second part runs from the s3 to the basal plate (e.g. in *Ephoron virgo*), but not to the PNP as Matsuda assumed.

Tsui & Peters (1972) also described the abovementioned muscle. According to their description the muscle is attached to the median plate running to the subalare. But presumably the right dorsal attachment is not the median (or basal) plate but rather the (not identified) third wing base sclerite (s3). Furthermore, they assumed that this muscle serves to transmit the pull exerted by the subalar muscles in depressing the wings. Nevertheless, according to a personal communication of Matsuda, the authors did not conclude a homology between Ax.PmS and the muscle of the 3Ax of Neoptera, but regardless of a similar function and position of these muscles assumed their convergent development in Ephemeroptera and Neoptera. Matsuda (1956) tried to homologise s5 with 3Ax and Ax.PmI with the wing flexor of Neoptera with an unlikely and not parsimonious argumentation. Thus, he did not recognise the similarity of the muscle, which is described by Tsui & Peters (l.c.) and the muscle attaching to the 3Ax of Neoptera.

The s2 is partly the same as the sclerite B of Brodsky (1970), which morphologically and functionally corresponds to the 1Ax of Neoptera.

The insertion of a pleural muscle, the connection to Sc, the sclerotisation in the dorsal wing membrane, and the convex axillary flexion-line posterior to s2 are characters that point at a homology of s2 with the first axillary sclerite (1Ax) of Neoptera.

Proximal part of BP

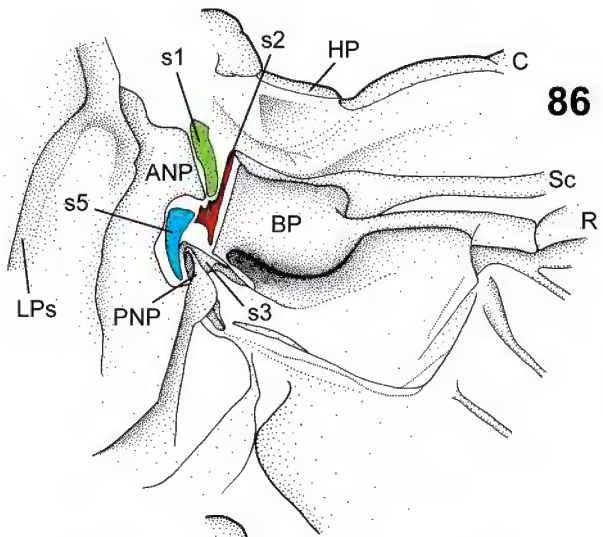
The 2Ax of Neoptera is characterised by the following: It is sclerotised in both dorsal and ventral layer of the wing membrane, no muscle is attached to it (in the ground plan of Neoptera), ventrally it articulates with the PWP, it has a convex axillary flexion-line lying proximally, and is connected to the anterior radial vein, PMP and 3Ax.

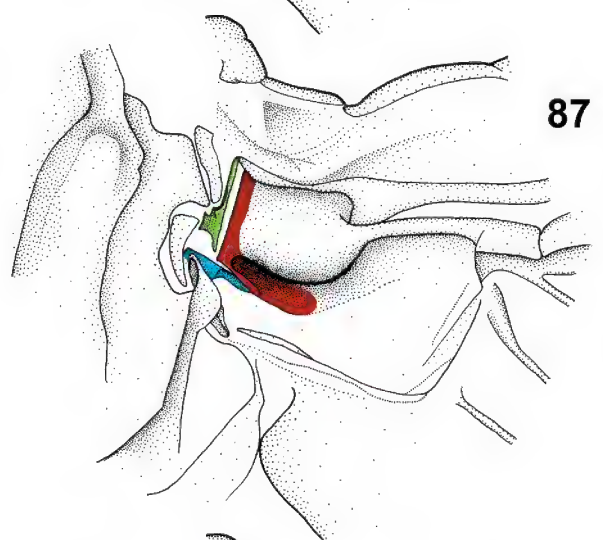
A homology of the proximal part of the basal plate (BP) of Ephemeroptera with 2Ax of Neoptera was assumed by Brodsky (1970: 185) who wrote: "The state of the second axillary sclerite in a mayfly nymph gives an objective representation of its shape (boomerang-shaped) and its connection with the remaining sclerites. In the imago the second axillary sclerite is fused with the median plate ...", but no further morphological grounds for a homology are given. Later he (Brodsky 1974) assumed, contradictory to his earlier view, that the loss of the connection between the 1Ax and the base of the subcostal vein is a specific character of Ephemeroptera since he suggested that the s1 (instead of s2 as proposed in his previous work) is homologous with the 1Ax of Neoptera. Furthermore, he assumed in his contribution of 1974 that the s5 in the wing base of several mayflies may be designated the median notal process that is not homologous with the median notal process of other orders, since the latter is articulated with the first axillary sclerite. But none of these two points is relevant if one postulates a homology of the s2 to the 1Ax and the proximal base of the BP to the 2Ax.

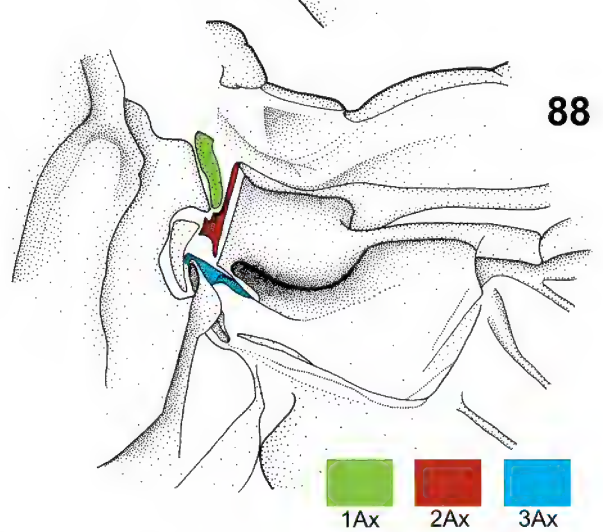
The homology of the basal plate (BP) with the second axillary sclerite is also proposed by Bekker (1954) who, however, homologised the whole BP with the 2Ax.

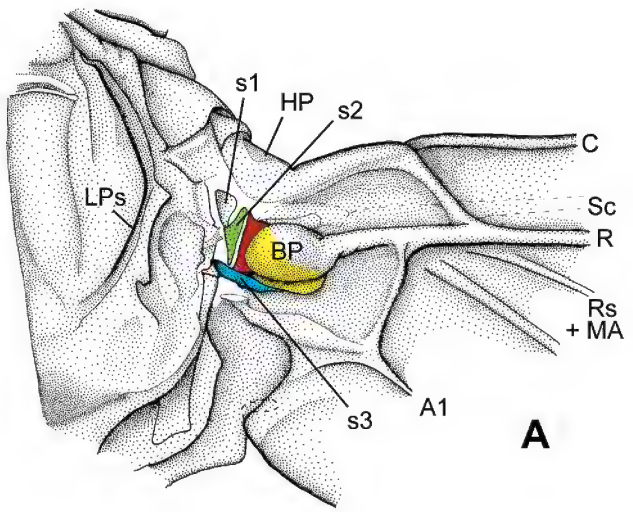
Based on the morphological data presented herein a homology of the proximal part of the basal plate to the 2Ax of Neoptera is evident since the first shows characteristics of the 2Ax of Neoptera.

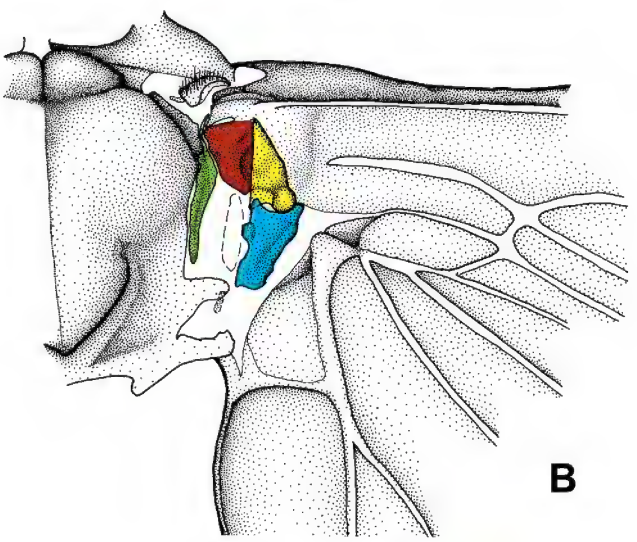
The proximal area of the BP is sclerotised in both the dorsal and ventral layer of the wing membrane. It possesses a process (BPp; Figs. 7–8, 32–33, 43, 93, 97) on its ventral side that articulates with the pleural wing process (PWP). The proximal flat area of the BP is connected to the anterior radial vein by the basal plate. In Plecoptera the anterior part of the 2Ax is sometimes partly or completely fused with the base of the anterior radial vein. For example, in *Pteronarcys reticulata* (Pteronarcyidae), the antero-distal part of the 2Ax is fused with the base of the radial vein over about one third of the length of the 2Ax

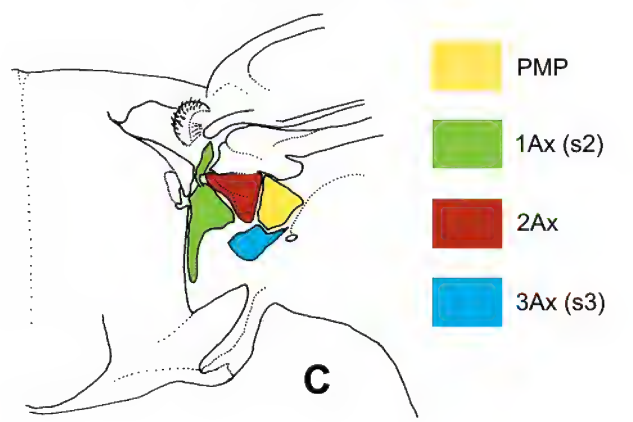






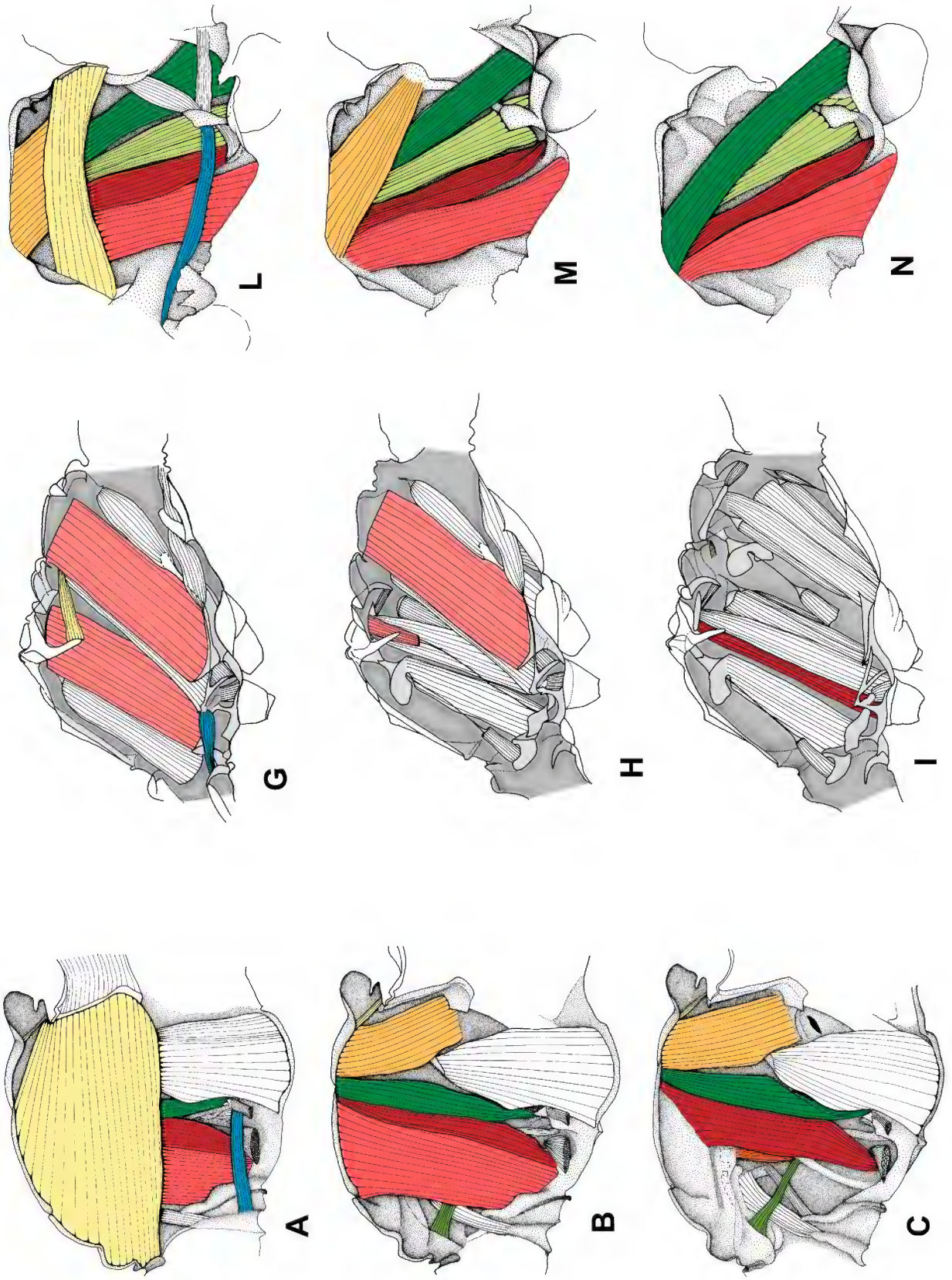






Figs. 86–88. Homology of the ephemeropteran wing base sclerites with the neopteran wing base sclerites (right fore wing of *Rhithrogena semicolorata*) (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: figs. 2–4). – **86**. After MATSUDA (1956). **87**. After BRODSKY (1970). **88**. After BRODSKY (1974).

Fig. 89. Homology of the ephemeropteran wing base sclerites with the neopteran wing base sclerites assumed in this work. – **A**. *Habroleptoides confusa* (Ephemeroptera), right fore wing. **B**. *Perlodes microcephalus* (Plecoptera), right hind wing. **C**. *Pteronarcys reticulata* (Plecoptera), right fore wing.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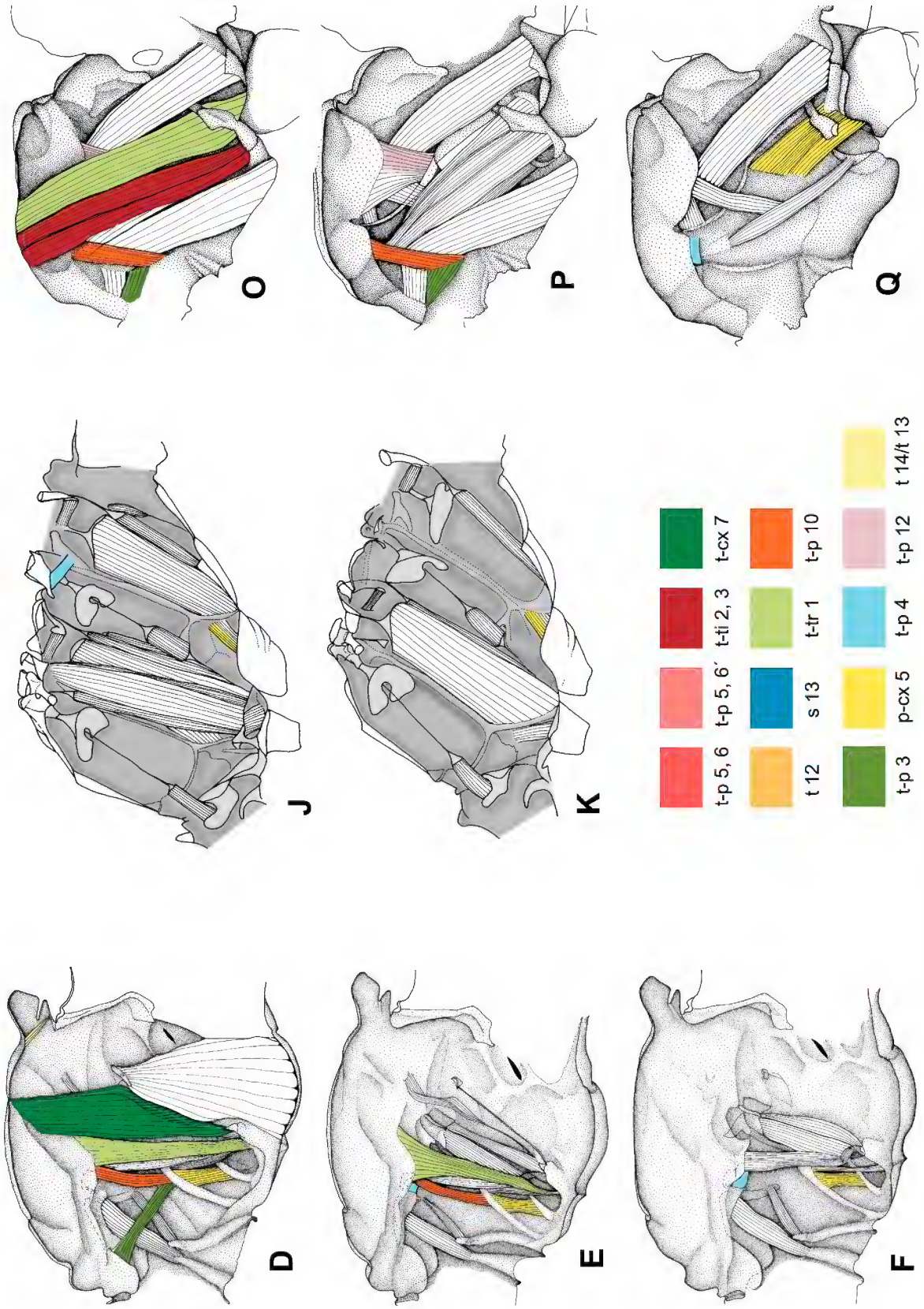
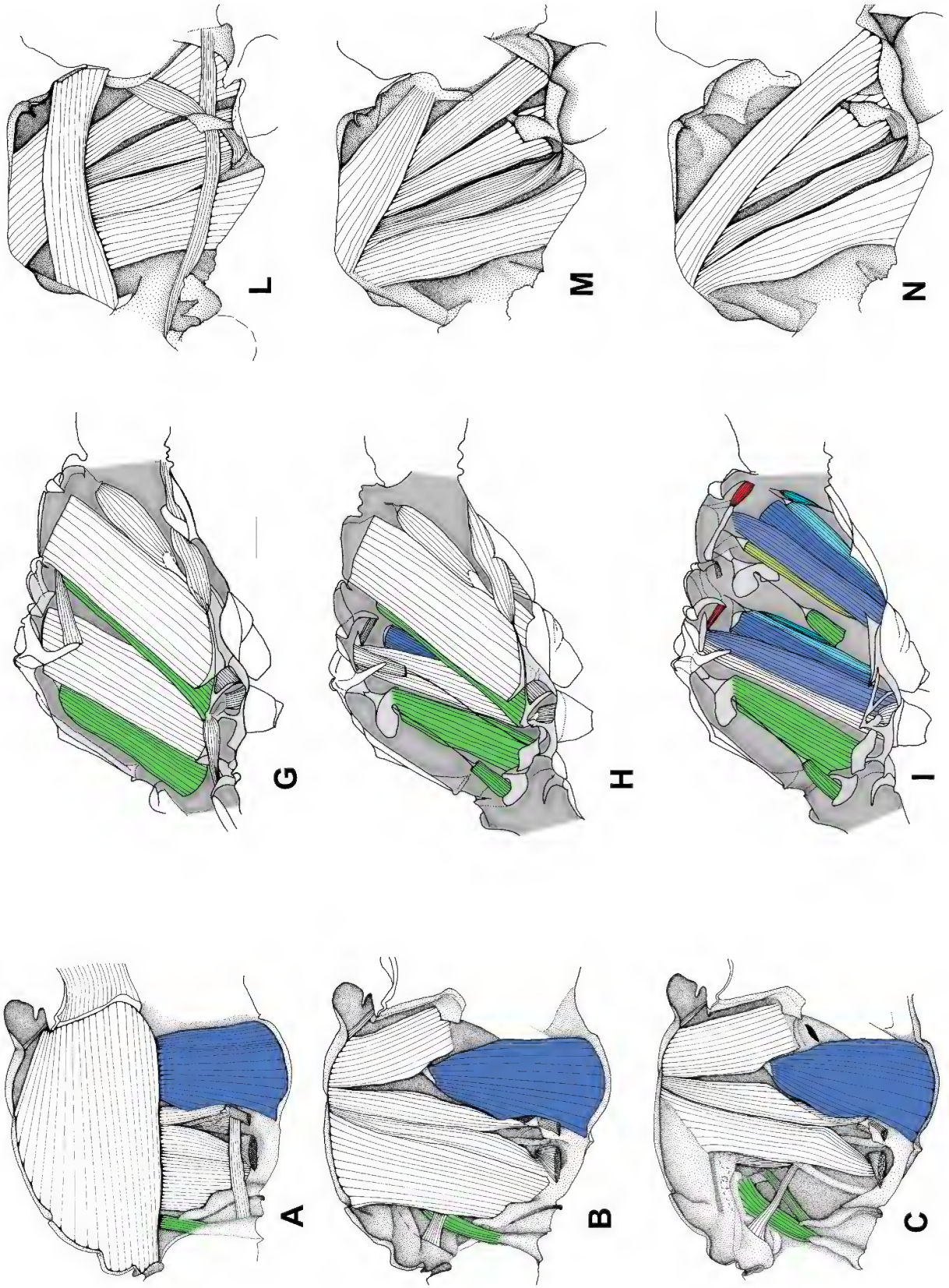


Fig. 90. Homology of the indirect flight muscles. – **A–F**. *Siphlonurus aestivalis* (Ephemeroptera), mesothorax. **G–K**. *Sympetrum* cf. *striolatum* (Odonata), synthorax. **L–Q**. *Brachyptera seticornis* (Plecoptera), mesothorax. * – t-p 5, 6´ – homology to t-p 5, 6 assumed.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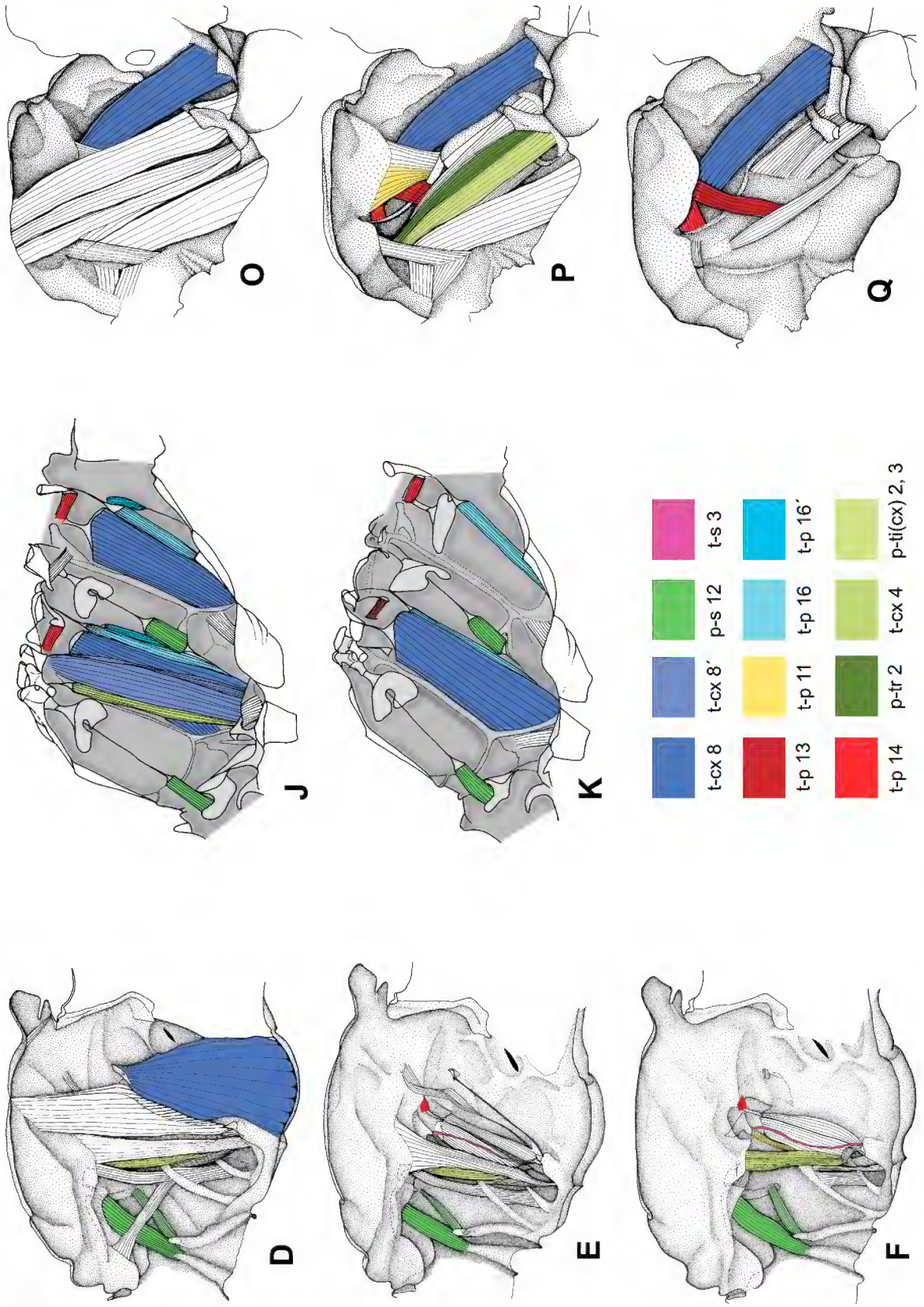
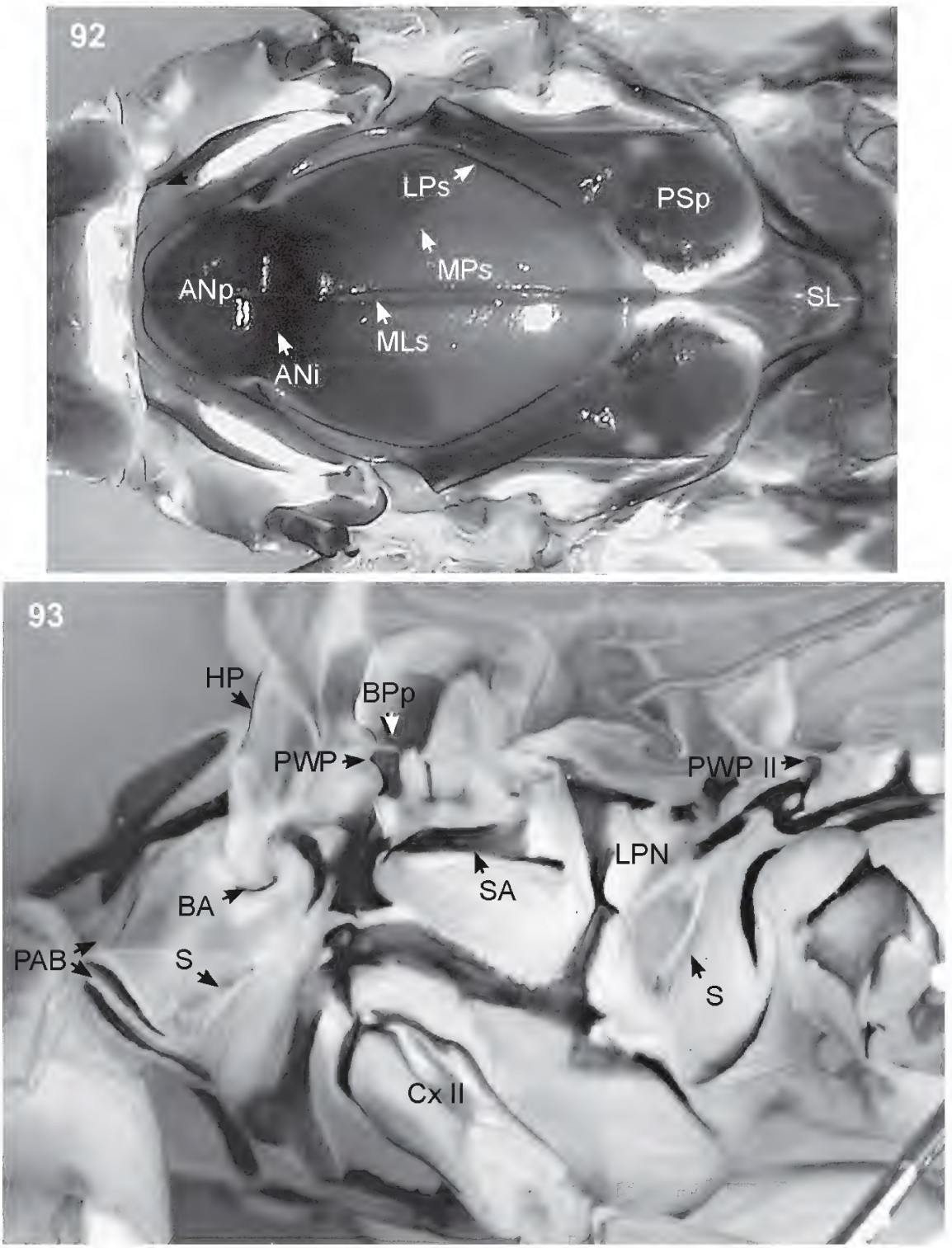
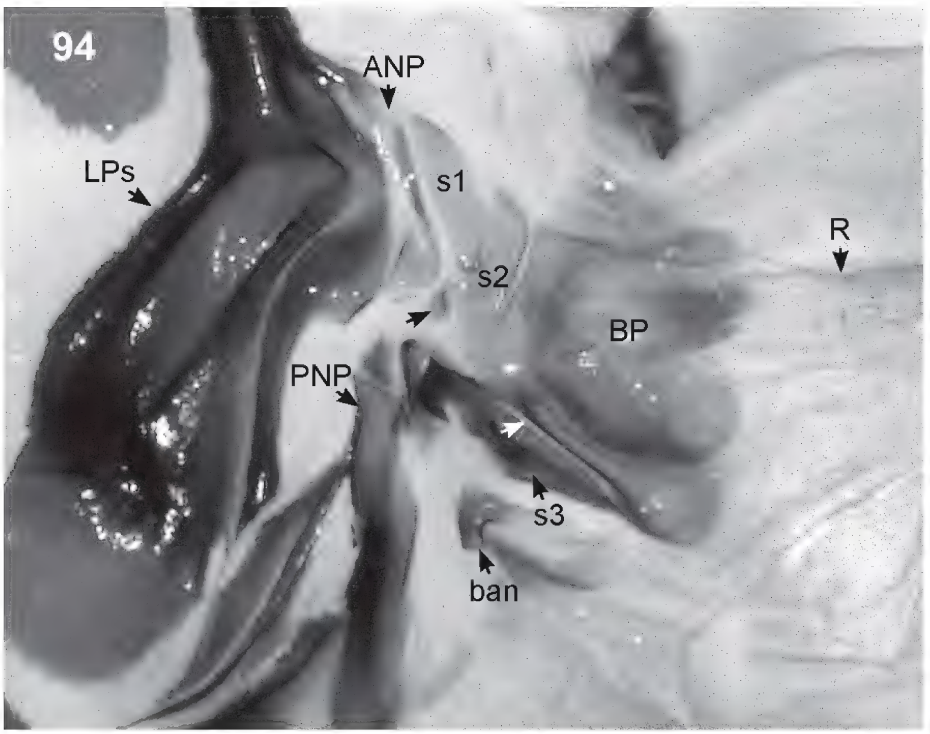
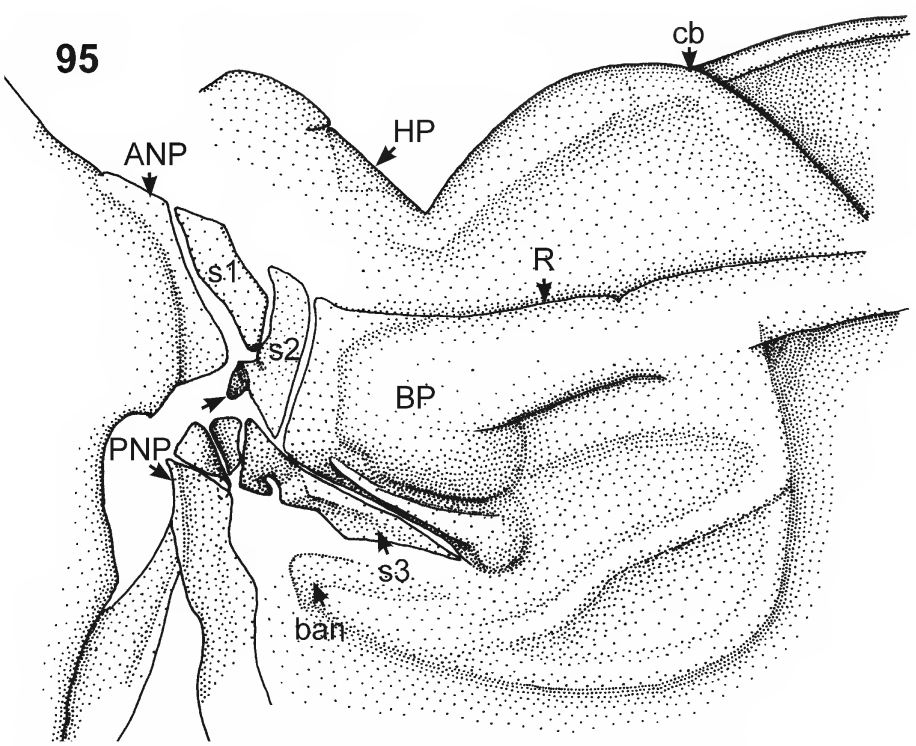


Fig. 91. Homology of the direct flight muscles. – **A–F**. *Siphlonurus aestivalis* (Ephemeroptera), mesothorax. **G–K**. *Sympetrum* cf. *striolatum* (Odonata), synthorax. **L–Q**. *Brachyptera seticornis* (Plecoptera), mesothorax. t-cx 8´ = most likely a separated part of t-cx 8; a possible homology of t-cx 4 and p-ti(cx) 2, 3 has to be further investigated; t-p 16 is also present in *B. seticornis* (compare Fig. 125, ppm 56).

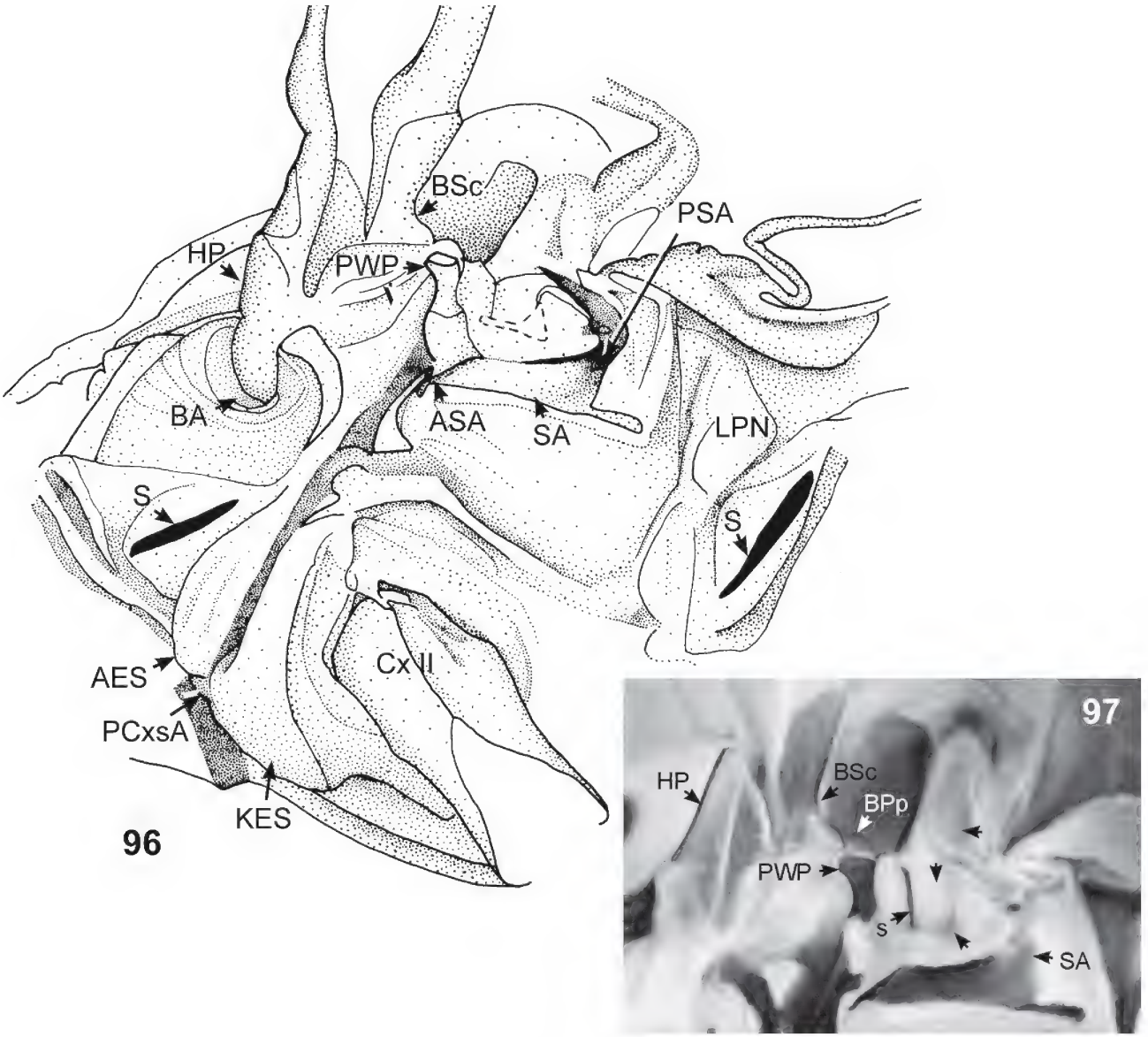


Figs. 92–93. *Ephemera danica*, mesothorax. – **92**. ♀ imago, dorsal view (head to the left). **93**. ♀ subimago, lateral view.





Figs. 94–95. *Ephemera danica*, ♀ subimago, wing base sclerites of fore wing. – The white arrow marks the membranous area that separates the basal plate from the third wing base sclerite (s3); the black arrow marks the proximal process of the second wing base sclerite (s2) that is bent inwards.



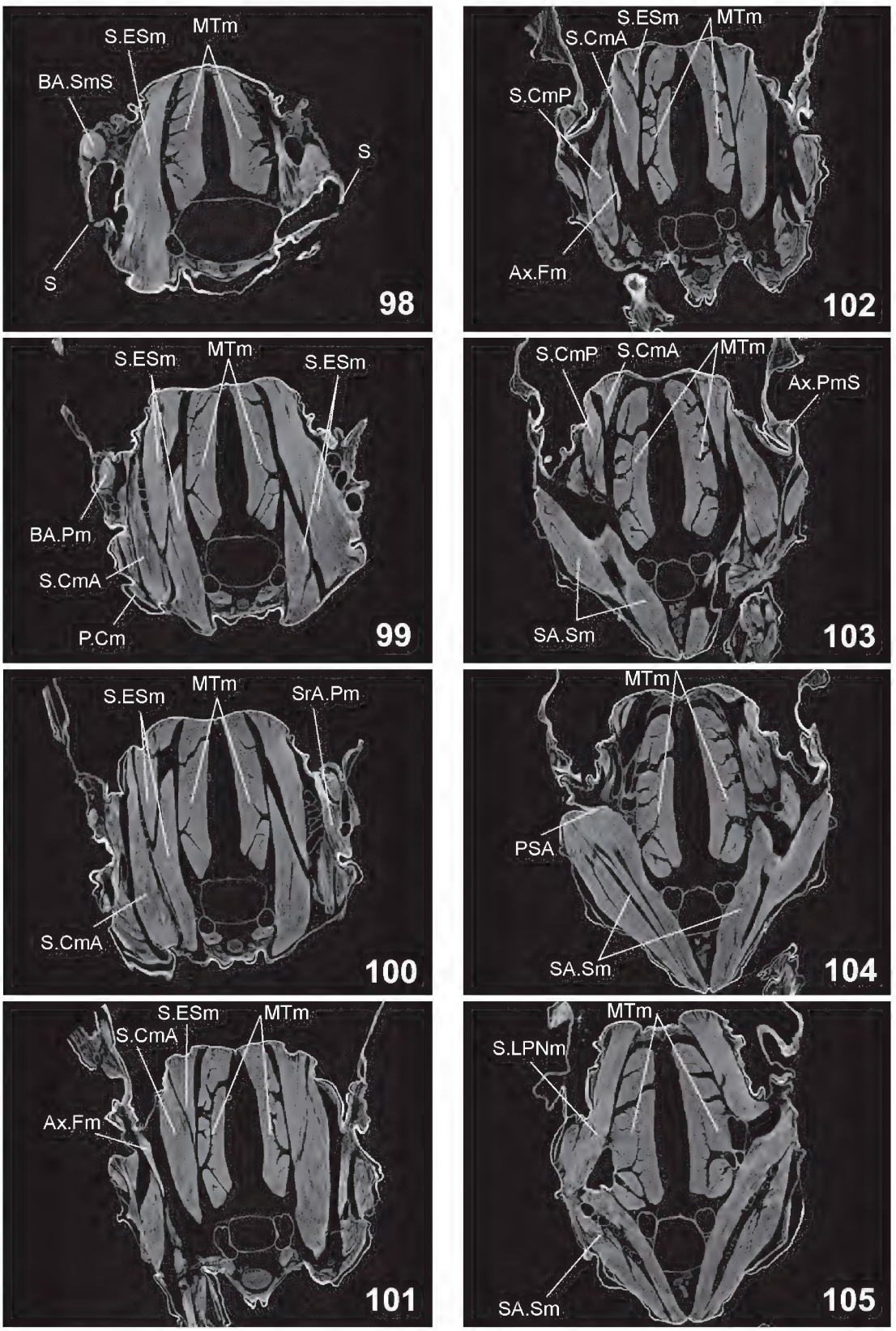
Figs. 96–97. *Ephemera danica*, ♀ subimago, mesopleurum. – **96**. Overview. **97**. Upper area. – s = anterior sclerite of the SA; the arrows, which are directed leftwards mark the s3 (3Ax) shining through the membrane; the arrow that is directed downwards marks the Ax.PmS shining through the membrane and is attached to s.

(Fig. 71). This fusion appears also in the hind wings of other Plecoptera and seems to be secondary (Willkommen & Hörnschemeyer 2007).

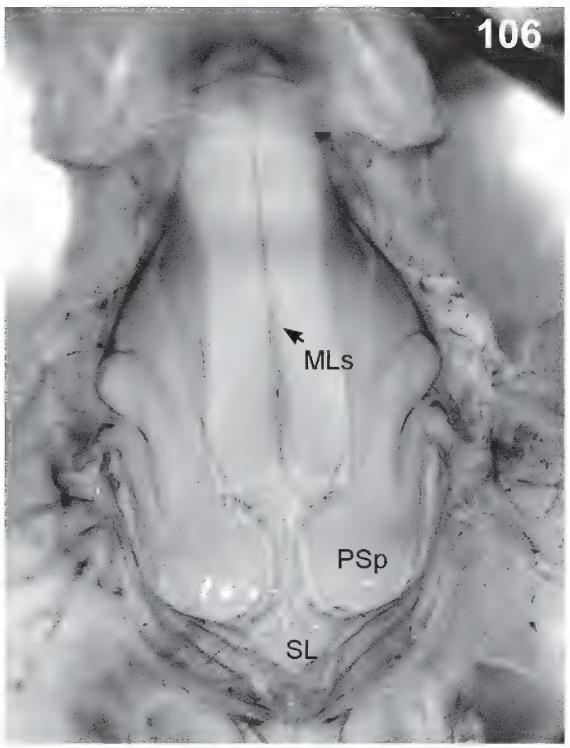
There is no muscle attached to the proximal part of the BP. This mirrors to the condition of the 2Ax of Neoptera. Furthermore, there is a convex flexion-line between the 1Ax and the 2Ax in Neoptera (Wootton 1979). This flexion-line lies between s2 and the proximal part of the basal plate in the ephemeropteran wing base. It indicates that s2 is homologous with the 1Ax and that the proximal part of the basal plate is homologous with the 2Ax of Neoptera.

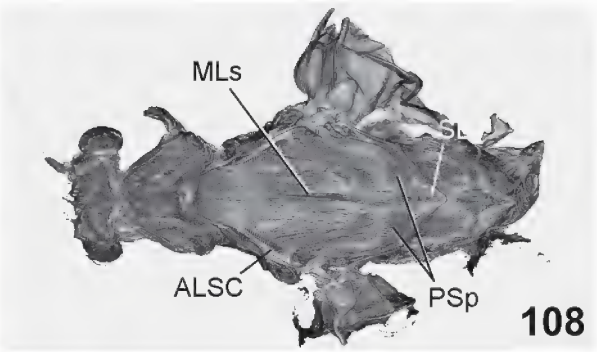
Third wing base sclerite – s3

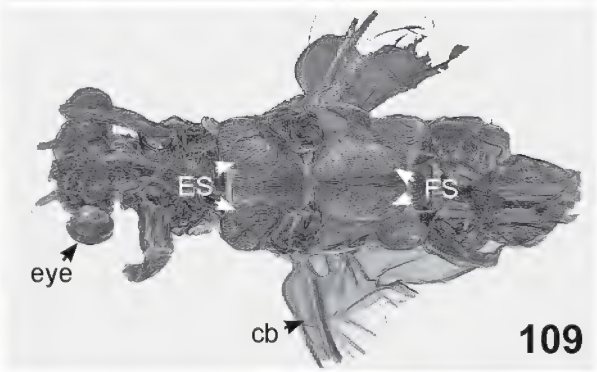
The third wing base sclerite (s3; Figs. 2–3, 27–29, 41, 94–95, 107) is without a doubt the homologous part to the 3Ax of Neoptera (Bekker 1954; Brodsky 1970, 1974, 1994; Willkommen & Hörnschemeyer 2007). It is sclerotised in the dorsal and partly in the ventral layer of the wing membrane. In most of the examined taxa this sclerite is connected to the posterior part of the BP and it is also associated with the anal veins via the basanale (ban) and the anal brace (ab). In the examined taxa the s3 is distinctly separate in *Ephemera danica* (Ephemeridae; Figs. 94, 95). If

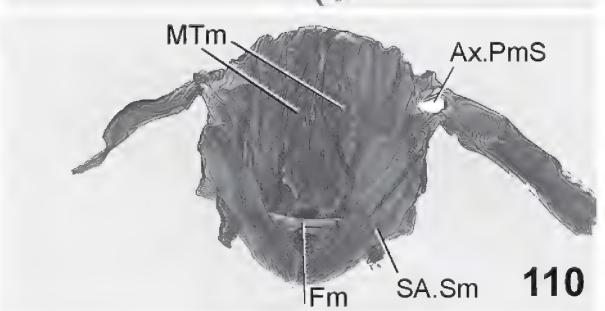


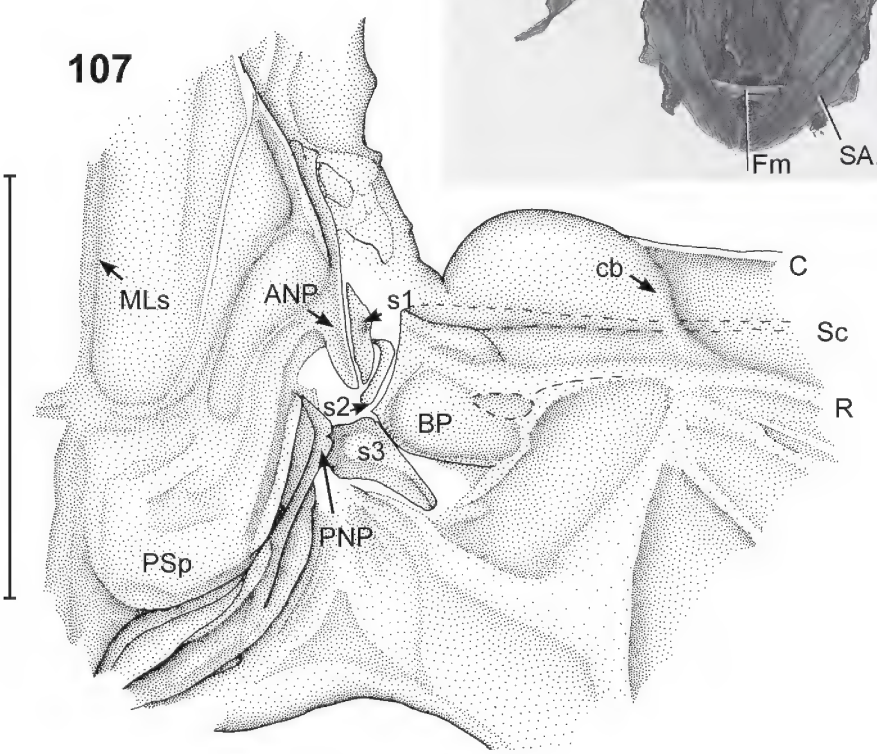
Figs. 98–105. *Ephemera danica*, ♀ subimago, mesothorax (µCT-data), cross sections from anterior (98) to posterior (105).



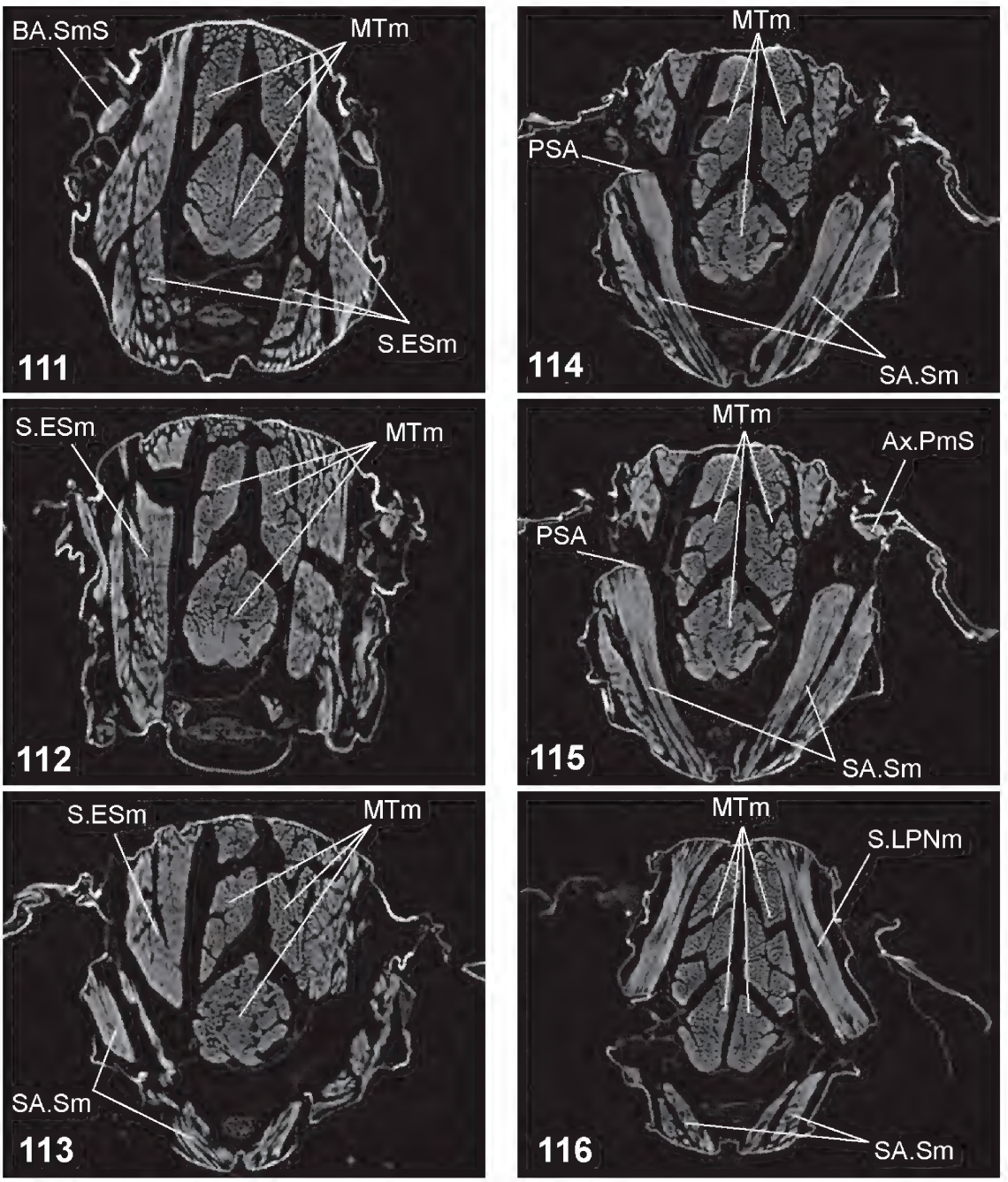








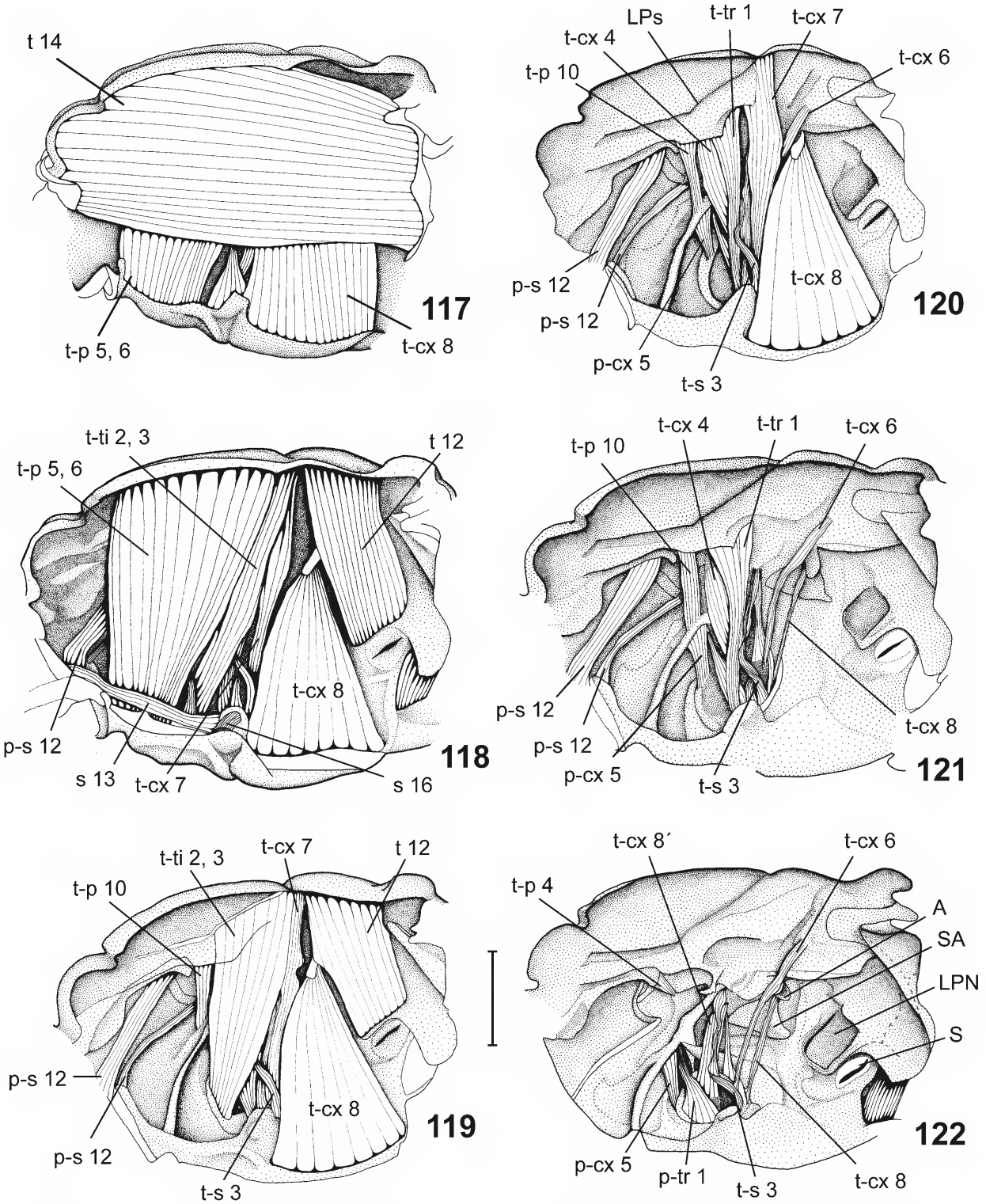
Figs. 106–110. *Exeuthyplocia minima*, ♂ imago. – **106**. Overview of the mesotergum. **107**. Wing base of the right fore wing. – **108–110**. Reconstruction of µCT-data. **108**. Thorax, dorsal view. **109**. Thorax, ventral view. **110**. Mesothorax, cross section posterior to the pleural suture, on a level with the SA and 3Ax. – Scale: 1 mm.



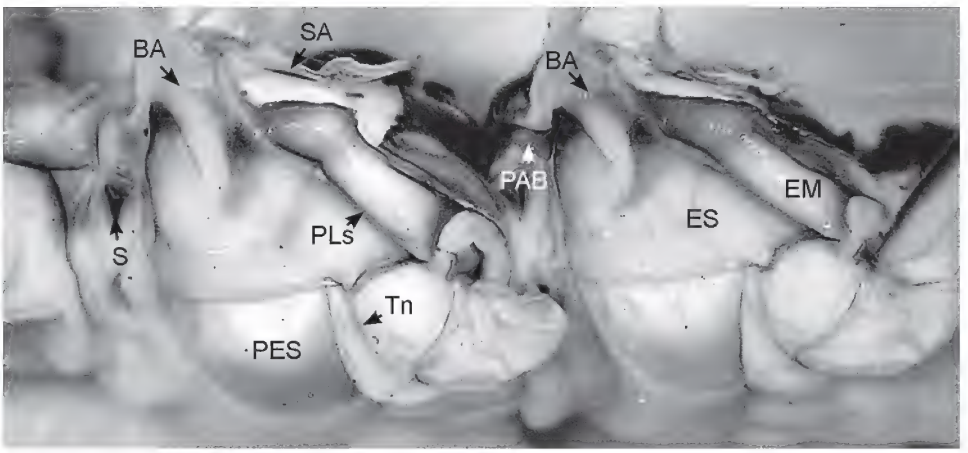
Figs. 111–116. *Exeuthyplocia minima*, ♂ imago, mesothorax (µCT-data), cross sections from anterior (111) to posterior (116).

not fused, s3 is more or less tightly associated with BP e. g. in *Siphlonurus aestivalis* (Siphlonuridae), *Ephoron virgo* (Polymitarcyidae), *Rhithrogena semicolorata* or *Ecdyonurus submontanus* (Heptageniidae). Ventrally the s3 is associated with the subalare (SA) as it is also the case in Neoptera. The orientation of the s3 in relation to the longitudinal body axis of the insects is nearly the same in Ephemeroptera and in Neoptera. But the most important point is that a muscle (Ax.PmS; Figs. 6, 7, 10, 54–55, 103, 110, 115) inserts on the s3, running to the pleurum (posterior to the PWP; Figs. 6, 7, 10, 97, 103). The Ax.PmS was documented by Grandi (1947), and also by Bekker (1954), Matsuda (1956), Tsui & Peters (1972), Kluge (1994) and Brodsky (1970, 1974, 1994). The "Musculus lateralis octavus mesothoracis" (II pm8) of Dürken (1907) might also be the Ax.PmS of the third axillary sclerite of Ephemeroptera.

Grandi (1947) termed the above-mentioned muscle



Figs. 117–122. *Habroleptoides confusa*, ♀ imago, musculature of the right half of the mesothorax at progressive stages of dissection, starting with median muscles (117) and progressively proceeding to the most lateral muscles (122) (modified after Willkommen & Hörnschemeyer 2007: figs. 12–17, terminology following Matsuda 1970). – Scale: 0.5 mm.



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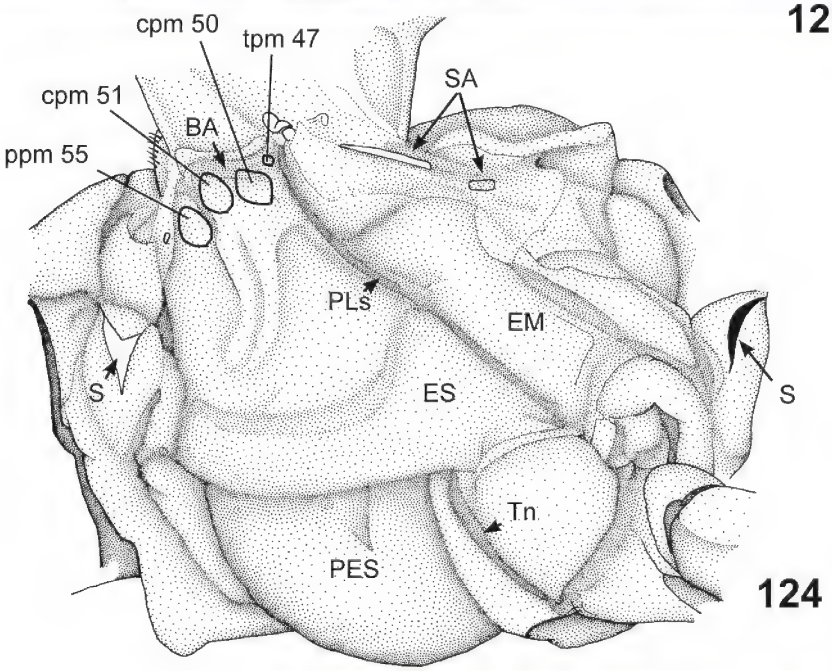

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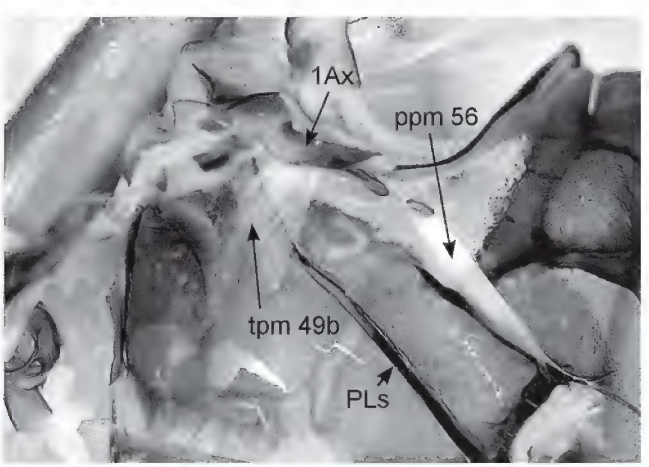

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Figs. 123–125. *Isoperla* spp., ♀, thorax, lateral view. – **123**. *I.* sp., meso- and metathorax. **124**. *I. grammatica*, mesothorax; encircled are the attachment points of several muscles that are attached to the basalar area. **125**. *I. goertzi*, right mesopleurum; tpm 49b = anterior part of tpm 49.

"pleurocondilo-scutellare" and KLUGE (1994) termed it axillar-pleural muscle superior (Ax.PmS). Both authors assumed that the axillary sclerites of Ephemeroptera are not homologous with that of Neoptera. GRANDI (1947: 105, 107) pictured the muscle in her figures XVII and XIX but she did not recognise the correlation to the 3Ax and its muscle in Neoptera because she did not identify the s3 as a separate sclerite. KLUGE (1994) neither mentioned the muscle in the text (except in the abbreviation list on p. 42) nor pictured it. As well as GRANDI, KLUGE did not homologise the axillary sclerites of Ephemeroptera and Neoptera whereby he overlooked the significance of the existence of this muscle. MATSUDA (1956: 106) mentioned a muscle that "stretches between the posterior notal process and the median plate" without any further discussion (see above). But he noted a muscle that is stretched between the s2 and the pleurum (Ax.PmI equivalent to his muscle 51) that shows a striking similarity to the wing flexor muscle in other pterygote insects, which usually inserts on the third axillary sclerite (see above). Therefore, he assumed that the muscle "may be regarded as the muscle of the third axillary sclerite judging from the correlation in the occurrence between the muscle and the third axillary sclerite and the point of attachment of the muscle to the second axillary sclerite. [...] but the above example clearly indicates that the insertion also tends to shift [...]" (MATSUDA 1956: 111). He homologised the s5 with the 3Ax though this sclerite shows no characteristics of the 3Ax of Neoptera. According to own observations the 3Ax of MATSUDA is neither associated with the anal veins nor with the subalare and no muscle is attached to the s5 and it is sclerotised only in the dorsal layer of the wing membrane. Moreover, sometimes it is attached to the tergum and is orientated almost parallel or slightly acute-angled to the longitudinal body axis. Therefore, the assumption of MATSUDA is not the most parsimonious one. He overlooked the fact that the s3 shows nearly all characteristics of the 3Ax of Neoptera (including the axillar-pleural muscle) because he did not identify the sclerite posterior to the BP probably since in most cases the s3 is not distinctly separate. TSUI & PETERS (1972) described the muscle stretched between the subalare and the median plate (II-22a of these authors). They described the right function of the muscle and assumed a convergent evolution of the similar function between Ephemeroptera and other Pterygota.

BEKKER (1954) supposed a homology only of 2Ax and 3Ax in Ephemeroptera and Neoptera. According to him, the 2Ax in Ephemeroptera is the whole basal plate (BP) and the 3Ax is s3. He described a muscle, of which the first branch runs from the 3Ax (s3) to the pleural ridge and the second branch stretched between 3Ax (s3) and a cavity of 2Ax (BP).

BRODSKY (1970, 1974, 1994) assumed without a doubt a homology of the muscle, running from the s3 to the pleurum, between Ephemeroptera and Neoptera (his muscle Pm14 in 1970, TPm5 in 1974 and t-p 14 in 1994) that helps to control the plane of impact (BRODSKY 1970: 187).

In Odonata there are two short muscles (29 and 30, respectively 51 and 52 in Figs. 62–66), which are attached to the postero-internal side of the axillary plate and to the membrane just behind the pleural wing process (ASAHINA 1954). These muscles are in the same position as the muscle running from the 3Ax to the pleurum (Ax.PmS) of Ephemeroptera and (t-p 14 sensu MATSUDA 1970) of Neoptera. Therefore, one can assume that a third axillary sclerite like that of Ephemeroptera and Neoptera is also present in Odonata but in the latter fused with some of the other wing base elements (for further interpretations of wing base elements in Odonata see below).

The third axillary sclerite (3Ax) in Plecoptera is rather simple in shape. The anterior arm is indistinct. In the fore and hind wings of *Pteronarcys reticulata* (Pteronarcyidae) the 3Ax is simple (Figs. 67–70, 72, 73) and likewise the 3Ax of the fore and hind wings of *Brachyptera seticornis* (Taeniopterygidae) (Figs. 74–77), *Leuctra hippopus* (Leuctridae) (Fig. 85), *Nemoura cinerea* and *Protonemura meyeri* (Nemouridae) is rather simple (own observations). The flexor muscle of the wing is stretched between a proximal concavity of the 3Ax and the pleural ridge next to the pleural wing process. In several Plecoptera the 3Ax is anteriorly partly or completely fused to the proximal median plate (PMP), for instance in the fore and hind wings of *L. hippopus*, *N. cinerea* and in the hind wings of *P. reticulata* and *B. seticornis* (own observations; Fig. 77). The fusion of the 3Ax and the PMP is most likely a secondary development in Plecoptera. Just as in Plecoptera, the close association of the s3 to the BP in the wing base of Ephemeroptera is presumably secondary, particularly since the s3 is not really fused in the examined Ephemeroptera. Actually in the basal *Siphlonurus aestivalis* the s3 is not even partly fused with the BP. In Ephemeroptera it could be an adaptation for stability in flight during the nuptial dances (see section 4.4).

In summary, the characteristics of the s3 are evidence of homology of the third sclerite (s3) of Ephemeroptera with the third axillary sclerite (3Ax) of Neoptera.

Fifth wing base sclerite – s5

In several Ephemeroptera there is a further sclerite in the wing base (s5) lying between the s2, the s3 and the PNP (Fig. 86). Its occurrence in different taxa of the Ephemeroptera (*Siphlonurus*, *Heptagenia*, and *Rhithrogena* after own observation, and also *Ametropus*, *Metretopus*, and *Parameletus* according to BRODSKY 1974) suggests that it might belong to the ground plan of Ephemeroptera. In the primordial taxon *Siphlonurus aestivalis* this sclerite is not completely detached from the scutum. Also in the examined *Rhithrogena semicolorata*

and *Ecdyonurus venosus* (own observations) and in *Ecdyonurus fluminum* (GRANDI 1947) it is not completely detached from the scutum. KLUGE (1994) termed it proximal axillary sclerite since he assumed that none of the wing base sclerites in Ephemeroptera are homologous with the axillary sclerites of Neoptera. MATSUDA (1956) stated a homology of this sclerite to the 3Ax. TSUI & PETERS (1972) mentioned that a third axillary sclerite (equivalent to s5) is present only in *Aprionyx* (see above) but they have not labelled a 3Ax in their drawings. The interpretations of BRODSKY (1974, 1994) are contradictory to each other. Within his investigation of *Ephemera vulgata* (BRODSKY 1970) no discussion of this sclerite is included because in *E. vulgata* as well as in the herein examined *E. danica* (Ephemeridae) the sclerite is absent. BRODSKY (1974) wrote that the suture between the scutum and the PNP acquires particular importance in the wing base of Ephemeroptera since it makes a rotation of the posterior part relative to the anterior part of the tergite possible. More mobility is possible due to a slit in this area that is connected in its turn with the s5. Therefore this sclerite (s5) is "... the portion of the tergite remaining on the site of the previously uniformly sclerotized division" (BRODSKY 1974: 35).

On the above mentioned grounds BRODSKY (1974: 35) assumed that the s5 may be designated the median notal process. Furthermore, he annotated that this median notal process is not homologous with the MNP of other orders since the latter does not articulate with the 1Ax. However, if the homology of the wing base sclerites is as assumed herein (or by BRODSKY 1970), it is quite probable that the s5 is the homologous part of the MNP of other insect orders. Nevertheless, regarding the last-mentioned fact one can arrive at a further conclusion: The s5 could also be a detached or rather a not yet associated posterior part of the 1Ax as it is present in Neoptera. BRODSKY (1994) came to exactly this conclusion because he hypothesised, contrary to his previous work (BRODSKY 1974) that the s2 instead of the s1 is the homologous sclerite to the 1Ax of Neoptera whereas he gave no reasons for his different interpretations.

Wing base of Odonata

The wing base of Odonata is characterised by the presence of two plates (hp and axp in Fig. 58), of which the anterior plate is not composed of axillary sclerites (1Ax, 2Ax and 3Ax). The axillary plate of Odonata is indirectly connected to the subcostal vein (Sc). Furthermore, the anterior radial vein (R), the radial sector (Rs) and the anterior medial vein (MA) as well as the posterior medial veins (MP) and the cubital veins (Cu) are associated with the axillary plate. The anal veins (A) are connected to the posterior part of the axillary plate. The posterior pleural wing process (PWP; Figs. 59, 60), which is most likely the homologous structure to the PWP of other orders (TANNERT 1958) is connected to the antero-ventral part of the axillary plate. A muscle is attached to the posterior part of the axillary plate running to the pleurum next to the posterior PWP (29 and 30, respectively 51 and 52 in Figs. 62–66), which is without much doubt homologous with the wing flexor (t-p 14 sensu MATSUDA 1970) of other Pterygota. On the assumption that the wing base is composed of several axillary sclerites in the ground plan of Pterygota that are arranged approximately as in the extant Plecoptera, the condition of Odonata could have been evolved as follows: As an adaptation to their manoeuvrable flight and to strengthen the wing base at least the 2Ax (connection to R and PWP), 3Ax (connection to A and "flexor" muscle), and the PMP (connection to M and Cu) are fused to the characteristic axillary plate. Whether the 1Ax is also fused to the axillary plate is unclear. The sclerite that is proposed the homologue of the 1Ax of Neoptera by TANNERT (1958) is not the 1Ax but rather the prescutum (see section 4.3). Furthermore, the basalare is enlarged in the wing base of Odonata and partly represents the humeral plate.

Conclusions

The assumption of a secondary strengthening of the wing base sclerites in Ephemeroptera and Odonata based on a ground plan with four wing base sclerites is more probable than their secondary fragmentation in Neoptera based on a ground plan with a mayfly-like wing base. This study agrees for the most part with the assumption of BRODSKY (1970) and partly with that of BEKKER (1954) and BRODSKY (1994). Based on morphological data presented herein a well-founded homology of the wing base sclerite is suggested as follows:

The homologous structure to the 1Ax of Neoptera is the second free wing base sclerite (s2) of Ephemeroptera (Fig. 89). The proximal part of the basal plate is proposed as homologous with the 2Ax of Neoptera. The distal and convex part of the basal plate is most likely homologous with the proximal median plate (PMP) of Neoptera. The third free wing base sclerite (s3) of Ephemeroptera is homologous with the 3Ax of Neoptera.

Ephemeroptera possess two to three axillary muscles. The first axillary sclerite (1Ax) is provided with two muscles in basal taxa (e. g. *Siphlonurus aestivalis*). The first muscle runs to the furca and the second one is attached to the pleurum. The latter muscle is absent in higher ephemeropteran taxa. Nevertheless, an axillar-pleural muscle (t-p 11) running from the 1Ax to the pleurum is present in all examined Plecoptera and regarded as a ground plan character of Pterygota. MATSUDA (1970) hypothesised that the axillar-furcal muscle (Ax.Fm) is an archaic muscle that is present in Lepismatidae and seems to be reduced in Neoptera.

In Ephemeroptera no muscle is attached to the second

axillary sclerite and also the second axillary sclerite of Plecoptera and other basal Neoptera is not provided with a muscle.

A short muscle (t-p 14), running to the pleurum just posterior to the PWP, is attached to the third axillary sclerite (s3) in Ephemeroptera. This muscle is homologous with one of the wing flexor muscles of Neoptera that is also attached to the 3Ax in this taxon. Thus, the axillar-pleural muscle of the third axillary sclerite is a ground plan character of Pterygota. Furthermore, the wing base is probably composed of at least three axillary sclerites and a proximal median plate in the ground plan of Pterygota.

The strengthening of the wing base in Ephemeroptera includes the fusion of the 2Ax with the PMP and the close association of the 3Ax with both the fused 2Ax and PMP. Furthermore, both the costal brace and anal brace strengthen the wing base.

4.3 Homology of the flight musculature (Figs. 90, 91, Tab. 3)

4.3.1 General Remarks

The pterothorax of Ephemeroptera is specialised and adapted to their typical kind of flight. Some of the indirect mesothoracic muscles are enlarged whereas the metathorax, the hind wings and the metathoracic muscles are partly reduced in size. Ephemeroptera are distinguished from the remaining Pterygota by the presence of the subalar-sternal muscles (SA.Sm, SA.Fm) and an axillar-sternal muscle (Ax.Fm) and, furthermore, by the absence of both a posterior subalar-pleural muscle and a basalar-trochanteral muscle. Moreover, in contrast to the Neoptera, the Ephemeroptera have two basalar-sternal muscles (BA.SmS, BA.SmI). In the Plecoptera (Neoptera), SA.Sm, SA.Fm, Ax.Fm, BA.SmS and BA.SmI are absent. Generally, the presence of the subalar-sternal muscles and the axillar-furcal muscle are regarded as plesiomorphic characters of Ephemeroptera.

4.3.2 Dorsal muscles

The main longitudinal muscle (**MTm**, t 14; Figs. 14, 35–37, 50, 98–105, 110–117) is very large in Ephemeroptera, which alludes to a good flight ability of Ephemeroptera. Usually, the anterior attachment ranges from the phragma to the posterior part of the scutum. Furthermore, the phragma between the mesothorax and the metathorax is enlarged in Ephemeroptera and provides a large posterior attachment for the MTm. This phragma is yet even extended posteriorly in *Oligoneuriella rhenana* (Oligoneuriidae) and serves as attachment to a massively enlarged MTm (own observation). The enlargement leads to a faster downstroke of the wings. Together with the also enlarged S.ESm, which leads to a faster upstroke of the wings it is an adaptation to a flight with a high wing beat rate. Oligoneuriidae are indeed characterised by a rapid horizontal flight instead of vertical nuptial dances (see section 4.4). Nevertheless, in *Ephoron virgo* (Polymitarcyidae), which is characterised by a flight behaviour resembling that of *O. rhenana*, this muscle is not exceedingly large.

The main longitudinal muscle of Plecoptera (t 14 sensu Matsuda 1970, dlm 35 sensu Wittig 1955; Fig. 78) is distinct but not enlarged as in Ephemeroptera. In Odonata there is only one dorsal longitudinal muscle (25 in Fig. 61), which is very weak and sometimes even absent in the metathorax (e. g. *Sympetrum* cf. *striolatum*, own observation; *Davidius nanus*, following Asahina 1954). The anterior attachments of the left and the right muscle are close to each other but the muscles diverge posteriorly. Matsuda (1970) named this muscle t 19, because he assumed it to be confined to Odonata. A homology of t 19 to muscles 11 and 12 of *Lepismachilis* sp. is hypothesised by him, whereas the t 14 (MTm) is homologised with muscle 4 and 5 of *Lepismachilis* sp. Nevertheless, one can also assume that t 19 of Odonata is the homologous muscle to t 14, which is also Brodsky's (1994: 109f) assumption. According to this author only the indirect flight muscle t 14 of recent Odonata can be reliably homologised with those of other insects.

In almost all Ephemeroptera examined the oblique dorsal muscle (**S.LPNm**; Figs. 15, 16, 51, 52, 105, 116; t 12 in Figs. 118, 119), dorsally attached to the posterior scutal protuberance (PSp; Figs. 1–3, 26, 38, 39, 92, 106–108) is a large muscle that extends in a nearly vertical course. Only in *Centroptilum luteolum* (Baetidae) it is rather weak and narrow, however, in contrast to the remaining examined Baetidae e. g. *Baetis* sp. and *Cloeon dipterum* where S.LPNm is about similar in size to that of other Ephemeroptera (own observation). In *Exeuthyplocia minima* (Euthyplociidae) the oblique dorsal muscle is also slightly weaker than in other mayflies, though with a rather large dorso-ventral extent since the ventral point of attachment is extended ventrally (own observation; Fig. 116). The orientation of the oblique dorsal muscle in Plecoptera (dlm 36 sensu Wittig 1955) is rather plesiomorphic since it runs obliquely backwards and is stretched between the anterior/middle part of the scutum and the second phragma (Fig. 79). The orientation of the nearly vertically running oblique muscle in Ephemeroptera is likely a derived character state.

In a few of the examined species, there is a third weak muscle running from the notum to the postnotum (t 13; Figs. 14–17). In contrast to *Siphlonurus columbianus* (Matsuda 1956) and *Siphlonurus linnaeanus* (Brodsky 1974) where t 13 was not observed, it is present in *Siphlonurus aestivalis* (Siphlonuridae). It is also present in *Serratella ignita* (Ephemerellidae) and most pronounced in *Ephemera danica* (own observations). According to (Brodsky 1994: 14), t 13 could be the detached uppermost

Tab. 3. Terminology of the thoracic musculature used by different authors with the underlying homology assumed in this work. – "BA" = crescent-shaped sclerite of Ephemeroptera, homology to a part of hp of Odonata assumed, homology to BA of Neoptera uncertain; * = BA.Trm not found in examined Ephemeroptera; ? = homology to ephemeropteran muscles uncertain.

Muscle attachments	Kluge 1994 (Ephemeroptera)	Matsuda 1970	Wittig 1955 (Plecoptera)
phragma I–phragma II	MT.m	t 14	dlm 35
scutum–postnotum	S.LPNm	t 12	dlm 36
scutum–postnotum		t 13	dlm 37
scutum–episternum	S.ESm	t-p 5, 6	dvm 40
scutum–trochantinus/scutum–Cx anterior	S.CmA	t-ti 2, 3	dvm 41
scutum–trochanter	S.Trm	t-tr 1	dvm 42
scutum–Cx posterior	S.CmP	t-cx 7	dvm 43
scutellum–Cx posterior	PSL.Cm	t-cx 6	–
notum–pleurum	AN.Pm	t-p 3	tpm 46a
subtegula–episternum	"BA.Pm"	t-p 4	tpm 47
ANP–episternum	SrA.Pm	t-p 10	tpm 46b
lateroscutum–pleurum	–	t-p 12	tpm 49a
episternum–Cx anterior	P.Cm	p-cx 5	cpm 52
episternum–trochanter	P.Trm	p-tr 1	
left mesofurca–right mesofurca	Fm	s 16	–
profurca–mesofurca	iFm	s 13	vlm 38
furca–Cx anterior	F.CmA	s-cx 5	bm 59
furca–Cx posterior	F.CmP	s-cx 2	
"BA"–sternum	BA.SmS	p-s 12	–
"BA"–sternum	BA.SmI	p-s 12	–
sclerite of scutum–coxa	BA.Cm	t-cx 4	cpm 51?
BA–trochanter*	BA.Trm	p-tr 2	cpm 50?
SA–furcasternum	SA.Sm	t-cx 8	
SA–furca	SA.Fm	t-cx 8	
SA–Cx posterior		t-cx 8	cpm 53
"SA"–Cx lateral	SA.Cm	–	–
posterior SA-pleurum	–	t–p 16	ppm 56
1Ax–furca	Ax.Fm	t-s 3	–
1Ax–pleurum	Ax.PmI	t-p 11	tpm 49b
3Ax–episternum	–	t-p 13	tpm 48a
3Ax–pleurum/epimeron	Ax.PmS	t-p 14	tpm 48b

bundle of the dorsal longitudinal muscle t14, which is indeed most likely.

4.3.3 Dorso-ventral muscles

Usually, the **S.ESm** (Figs. 14, 15, 35, 36, 50, 51, 98–102, 111–113; t-p 5, 6 in Figs. 117, 118) is the largest of the dorso-ventral muscles in the mesothorax of Ephemeroptera. It is the most important antagonist to the well developed MTm. The dorsal attachment is stretched across the middle part of the scutum and the muscle becomes more slender ventrally. In *Oligoneuriella rhenana* (Oligoneuriidae) the S.ESm is conspicuous. Its ventral attachment is large since the episternum is distinctly extended ventrally in this taxon (own observation). The episternum of *Ephoron virgo* (Polymitarcyidae) bears a resemblance to that of *O. rhenana*, though the ventral attachment is not as wide in *E. virgo* (ES in Figs. 48, 49) as in *O. rhenana* (own observation). In both taxa, especially the latter, the S.ESm is enlarged together with the enlargement of MTm (see above). The corresponding muscle (dvm 40 sensu Wittig 1955) in Plecoptera (Figs. 78–80) is a distinct indirect flight muscle, though not as large as in Ephemeroptera.

According to Matsuda (1970: 66), the conspicuous indirect flight muscle of Odonata (muscle 23 sensu Maloeuf 1935 and Asahina 1954, t-s 10 sensu Matsuda 1970) is homologised with the muscle 64 of *Lepismachilis* sp. since it is "a genuinely tergosternal muscle from the first nymphal stage on, whereas t-p 5 (and t-p 6) is primarily a tergopleural muscle". Neither in Ephemeroptera nor in Plecoptera does a muscle stretch between the anterior part of the tergum and the sternum. In comparison with the configuration of muscles of the Ephemeroptera and the Plecoptera, it becomes apparent that the muscle 23 of Odonata is the homologue of t-p 5, 6 (S.ESm, dvm 40). The ventral attachment of t-p 5, 6 is shifted ventrally from the larval to the adult stages of Plecoptera (Wittig 1955). It would be conceivable that the ventral point of attachment of the muscle 23 in Odonata represents an apomorphic

condition. Furthermore, MATSUDA (1970: 66) described a muscle (t-s 7) that originates from the antero-lateral portion of the tergum and inserts on the antero-lateral corner of the sternum. It is assumed that t-s 7 occurs in *Ecdyonurus* (Heptageniidae) and may also be present in Phasmida (MATSUDA 1970), thus, a homology to the muscle 23 of Odonata is also possible. Nevertheless, in none of the examined ephemeropteran taxa such a muscle is present.

In the Zygentoma (*Lepisma*, *Lepismachilis*) a lot of dorso-ventral muscles occur. Therefore, it is difficult to answer the question, which muscles occurred in the last common winged ancestor and whether the condition of muscle configuration of adult and larval Odonata represents the primitive state. Nevertheless, in the proposed sister groups, there is no anterior tergo-sternal muscle.

The scuto-coxal muscles (**S.CmA**, **S.CmP**; Figs. 15–17, 51–53, 99–103; t-ti 2, 3 and t-cx 7 in Figs. 118–120) and the scuto-trochanteral muscle (**S.Trm**; Figs. 17, 18, 52; t-tr 1 in Figs. 120, 121) are not as large as the S.ESm in Ephemeroptera. In contrast to the larvae, the scuto-trochanteral muscle is the weakest of the three mentioned muscles in the winged stages of Ephemeroptera because the movement of legs becomes rather unimportant in the winged stages. Both the anterior and posterior scuto-coxal muscle are about equal in proportion in Ephemeroptera. As in Ephemeroptera, only one muscle is attached to the anterior area of the coxa in Plecoptera. This muscle, dvm 41 (M. tergo-trochantinalis sensu WITTIG 1955) is ventrally attached to the trochantinus.

In *Lepisma* sp. there are three muscles running from the middle or anterior part of the tergum to the trochantinus (muscles 71–73 sensu MATSUDA 1970). Two further muscles are attached to the anterior margin of the coxa (muscles 61–62 sensu MATSUDA 1970). Three muscles are attached to the posterior margin of the coxa (muscles 63–65 sensu MATSUDA 1970). BRODSKY (1994) assumed that three anterior tergo-coxal muscles (t-ti[cx] 1–3 including trochantinal muscles) and two posterior tergo-coxal muscles (t-cx 6–7) are present in primitive winged insects. In contrast, MATSUDA (1970) proposed that three posterior muscles must be present in primitive pterygote taxa, based on the fact that MAKI (1938) has shown that the future subalar-coxal muscle is dorsally attached to the lateral margin of the tergum in the late embryo of *Leucophaea* (Blattaria) (see section 4.3.7). This assumption is possible because the subalare is not a detached part of the pleurum but rather a new formation, which originates directly below the wing pads. Based on this assumption, the wings have to be duplications of the tergite.

MATSUDA (1970) supposed that t-ti(cx) 2 and also t-ti(cx) 3 are present in the prothorax of Ephemeroptera and in the thorax of other insects. Furthermore, he homologised t-ti(cx) 2 with dvm 41 of WITTIG (1955) and mentioned that t-ti(cx) 2 sometimes inserts on the anterior margin of the coxa. It is assumed that the t-ti(cx) 3 is present in all thoracic segments of Ephemeroptera (MATSUDA l. c., BRODSKY 1994). If only one of those muscles is present, it is difficult to distinguish between t-ti(cx) 3 and t-ti(cx) 2 (MATSUDA l. c.). Since the trochantinus is probably reduced in Ephemeroptera, and most likely also in Odonata, it is difficult to ascertain whether the anterior tergo-coxal muscle of Ephemeroptera is rather the t-ti(cx) 2 or – more likely – the t-ti(cx) 3.

In Odonata, a muscle is distinguishable from the muscles 23 and 23′, which is attached to the scutum and to the antero-lateral margin of the coxa. This third part of the large indirect flight muscle (23) is most likely the corresponding muscle to muscle 37, though MALOEUF (1935) wrote that this muscle and the metathoracic muscle 60 are absent in adult Odonata. He examined the musculature of adult and larva of *Plathemis lydia* and *Anax junius* (Anisoptera). In contrast, ASAHINA (1954) summarised that both muscles (37 and 60) are absent in Zygoptera but present in Anisoptera and also in *Epiophlebia*. The musculature of adult *Epiophlebia superstes* (Anisozygoptera), *Davidius nanus* (Anisoptera) and *Mnais strigata* (Zygoptera) provided the basis for his assumption. Nevertheless, a muscle 37 is also present in *Sympetrum* cf. *striolatum* (Anisoptera), which is closely connected to the muscle 23 in this taxon (own observation; Fig. 63). Though muscle 37 is not present in Zygoptera that are supposed to have a lot of primitive characters, it is most likely a ground plan character of Odonata since it was found in *Epiophlebia*. Furthermore, a corresponding muscle is present in Ephemeroptera and Plecoptera. MATSUDA (1970) homologised muscle 37 of Odonata with the t-cx 6 or t-cx 7, but it is probably rather t-cx 3 (or t-cx 2) since the dorsal point of attachment of muscle 26 (coxobasalar see below) lies lateral to that of muscle 37 and the ventral attachment is on the lateral rather than the posterior margin of the coxa.

Only one tergo-trochanteral muscle is described in *Lepisma* sp. (Zygentoma). Consequently, MATSUDA (1970) homologised it (muscle 52 of *Lepisma* sp. of this author) with the tergo-trochanteral muscle of winged insects (dvm 42 sensu WITTIG 1955, t-tr 1 sensu MATSUDA 1970, S.Trm sensu KLUGE 1994). A tergo-trochanteral muscle is missing in the pterothorax of Odonata. It is most likely reduced, as it is also present in Ephemeroptera and in Plecoptera.

The second posterior tergo-coxal muscle of Ephemeroptera is the parascutello-coxal muscle (**PSL.Cm**), which is rather weak and tapering into a tendon-like ventral part. In *Ephoron virgo* (Polymitarcyidae) it lies more anteriorly and is slightly larger than in other taxa. Furthermore, it is almost as wide dorsally as it is ventrally in this taxon. In *O. rhenana* (Oligoneuriidae) the PSL.Cm is larger than in other ephemeropteran taxa (own observation). The latter two taxa are characterised by horizontal instead of vertical

nuptial dances. The differences to other mayflies concerning the PSL.Cm in these two taxa are likely associated with their horizontal flight. MATSUDA (1970) homologised the t-cx 6 with the PSL.Cm and t-cx 7 with S.CmP of Ephemeroptera. Furthermore, he assumed that the dvm 43 sensu WITTIG (1955) consists of t-cx 6 and t-cx 7. BRODSKY (1994) stated that both, t-cx 6 and t-cx 7 are present and separated in Plecoptera. This is indeed likely because in *Isoperla grammatica* (Perlodidae) and *Brachyptera seticornis* (Taeniopterygidae) there is a muscle (own observation), which is located posterior to t-cx 7 (dvm 43 sensu WITTIG 1955). MATSUDA (1970) wrote that t-cx 6 or t-cx 7 is present in Odonata, which is actually muscle 37 sensu ASAHINA (1954).

The anteronoto-pleural muscle (**AN.Pm**; Figs. 15–17), if present, is a weak muscle that consists only of a few fibres in Ephemeroptera. It corresponds to tpm 46a (sensu WITTIG 1955) and t-p 3 (sensu MATSUDA 1970).

The suralar-pleural muscle (**SrA.Pm**; Figs. 16–18, 53, 54, 100; t-p 10 in Figs. 119–121) is absent in *O. rhenana*, but in the remaining examined taxa it is a conspicuous muscle. MATSUDA (1970) homologised t-p 8 (muscle 45 in *Siphlonurus columbianus* sensu MATSUDA 1956) with SrA.Pm (sensu KLUGE 1994) but it is rather t-p 10. According to MATSUDA (1970: 63) t-p 8 connects the anterior margin of the basalare or of the episternum with the lateral scutal area anterior to the anterior notal wing process. However, the SrA.Pm of Ephemeroptera is dorsally attached to the ANP rather than anterior to it and runs to the anterior paracoxal suture of the pleurum. It is not associated with the basalare in Ephemeroptera. The t-p 10 (sensu MATSUDA 1970) is stretched between the pleural arm and the anterior notal wing process. Though a pleural arm is not developed in Ephemeroptera, the homologisation of the SrA.Pm with the t-p 10 is obvious.

MATSUDA (1970) assumed both t-p 8 and t-p 10 are present in Ephemeroptera, but in this area there is only one muscle (which is t-p 10, see above) in all Ephemeroptera examined. He referred to t-p 8 as muscle 45 (sensu MATSUDA 1956), however, t-p 10 is not mentioned in his publication of 1956 even though he examined a basal mayfly (*Siphlonurus columbianus*). MATSUDA (1970) homologised t-p 10 with II Pm 11 sensu KNOX (1935). Nevertheless, II Pm 11 (sensu KNOX 1935) is equivalent to muscle 45 (sensu MATSUDA 1956). Both muscles are homologous with t-p 10 rather than t-p 8. Furthermore, he homologised t-p 7 with tpm 46b of *Perla abdominalis* (sensu WITTIG 1955). The muscle t-p 7 connects the antero-lateral scutal area or the prescutal area with the lower part of the basalare (MATSUDA 1970: 62). According to WITTIG (1955) the tpm 46b of *Perla abdominalis* is stretched between the antero-lateral part of the scutum and the episternum. The tpm 46b of *Brachyptera seticornis* (Figs. 81, 82) is dorsally attached to the ANP and to the ridge at the anterior part of the episternum. The position of this muscle resembles SrA.Pm of Ephemeroptera and t-p 10 of Neoptera. Therefore, a homology of SrA.Pm, tpm 46b and t-p 10 is assumed. Nevertheless, t-p 7 and t-p 8 in other insects are probably the result of a splitting and can be traced back to a common origin.

4.3.4 Pleural muscles

A pleuro-coxal muscle (**P.Cm**; p-cx 5 sensu MATSUDA 1970) is present in all examined Ephemeroptera (Figs. 17–19, 53–55, 99; p-cx 5 in Figs. 120–122) and also in Odonata (36 in Fig. 66; muscle 36 sensu ASAHINA 1954) as well as in Plecoptera (cpm 52 sensu WITTIG 1955; cpm 52 in Fig. 83). In most of the previous contributions on musculature of Odonata no homologisation of the muscles is given. But even MATSUDA (1970) homologised the muscle 36 of Odonata with the p-cx 5 of other winged insects since a correlation is obvious.

The pleuro-trochanteral muscle (**P.Trm**; p-tr 1 sensu MATSUDA 1970) is present in Ephemeroptera (Figs. 17–19, 53–55; p-tr 1 in Fig. 122) and also in Odonata (39 in Fig. 66; muscle 39 sensu ASAHINA 1954), but it is absent in Plecoptera. MATSUDA (1970) homologised P.Trm with muscles 53 or 54 of *Lepisma* sp. Based on this assumption, the pleuro-trochanteral muscle is secondarily reduced in the pterothorax of most Neoptera. The same author also wrote that it is often present in the prothorax of Neoptera. This muscle is also reported in the pterothorax of Coleoptera, Homoptera, and Diptera. Its presence in Ephemeroptera and Odonata is a symplesiomorphic character of these two taxa.

In basal Neoptera, the furca is usually connected to the pleural arm by a muscle. This is also the case in Plecoptera, where the conspicuous mesothoracic furca is connected with the pleural arm by a distinct muscle (zm 61 sensu WITTIG 1955, p-s 1 sensu MATSUDA 1970). In Dermaptera, Plecoptera, Neuroptera and other Neoptera the pleural arm lies approximately in the middle of the pleural ridge. The location of the pleural arm in these orders roughly corresponds to the "*processus pleural* of CARPENTIER and BARLET" (MATSUDA 1970: 35). Furthermore, MATSUDA assumed in the same paper that p-s 1 is likely homologous with the muscle 27 of *Lepisma saccharina* (Zygentoma).

This muscle (p-s 1) is not present in Ephemeroptera at all. It is also lacking in adult Odonata. The reduction of this muscle is linked with the lack of a pleural arm in these taxa. MALOEUF (1935) mentioned a short muscle (muscle 35 sensu ASAHINA 1954) that is stretched between the furcal arm and the pleurum of larval Odonata. This muscle is absent in the adults. Most likely it is homologous to p-s 1 of other Pterygota.

As a pleural arm is well developed in Zygentoma (BARLET 1967) and basal Neoptera (MATSUDA 1970) its reduc-

tion must be assumed in Ephemeroptera and also in adult Odonata. This reduction can be supposed as a putative synapomorphic character of Palaeoptera where the muscle and the pleural arm are reduced in imagines of the stem group and in larvae of Ephemeroptera. But in all likelihood, the muscle (p-s 1) and the pleural arm are convergently reduced in Ephemeroptera and Odonata.

4.3.5 Ventral muscles

The intersegmental furcal muscle (**iFm**; s 13 sensu MATSUDA 1970) is present in the mesothorax of all examined Ephemeroptera (Figs. 14, 50; s 13 in Fig. 118), Odonata (41 in Fig. 61) and also in Plecoptera (vlm 38 sensu WITTIG 1955; Fig. 78) and other Neoptera (MATSUDA 1970). Thus, the iFm (sensu KLUGE 1994) corresponds to s 13 (sensu MATSUDA 1970).

The furcal muscle (**Fm**; s 16 sensu MATSUDA 1970) running from the left to the right furcal arm is present in the pterothorax of all examined Ephemeroptera (Figs. 14–16, 50, 51, 110; s 16 in Fig. 118). It is assumed to be also present in Phasmida, Blattaria, Mecoptera, Mallophaga and Heteroptera (MATSUDA 1970). This muscle was not found by me in the mesothorax of Plecoptera and Odonata.

The posterior furco-coxal muscle (**F.CmP**; s-cx 2 sensu MATSUDA 1970) is present in both mesothorax and metathorax of all examined mayflies (Figs. 18, 19, 36, 54). It also occurs in the thorax of other pterygote insects (MATSUDA 1970). **F.CmA** was listed by KLUGE (1994) in the abbreviation list but not mentioned in the text at all. However, fig. 5 of KLUGE pictures a muscle termed F.Cm, which was not found in the examined Ephemeroptera.

The muscle which connects the lateral area of the left and the right coxal margin (**Cx.Cxm** sensu KLUGE 1994) is present only in *Siphlonurus aestivalis* (Figs. 14–16) and absent in the remaining examined mayflies. It is assumed to be a derivate of s-cx 4, which is stretched between the spina and the posterior coxal margin that evolved by loss of the spina, although it may also be a modified s-cx 8 (MATSUDA 1970). This is likely although the muscle is attached to the anterior part rather than to the posterior part of the coxa in *S. aestivalis*.

A muscle that runs from the metafurca to the posterior part of the first abdominal segment or rather the anterior part of the second abdominal segment (s 20 sensu MATSUDA 1970) is present in the metathorax of *Siphlonurus aestivalis*, however, it is not listed in MATSUDA's (1970: 123f) table IV. According to the same author (1970: 74) it also occurs in "Thysanoptera, Homoptera, Mecoptera, Lepidoptera etc.".

4.3.6 Axillary muscles

The axillary apparatus is equipped with three muscles in the examined Plecoptera, and this has most likely to be assumed for the neopteran ground plan, too. The first muscle is stretched between the 1Ax and the pleurum (anterior part of tpm 49 sensu WITTIG 1955, tpm 49b in Fig. 82). Both second and third muscle of the neopteran axillary apparatus are dorsally attached to the 3Ax.

WITTIG (1955) could not verify the presence of a pleural muscle associated with the 1Ax in the pterothorax of *Perla abdominalis*. However, I could demonstrate its presence e.g. in *Isoperla grammatica*, *Isoperla goertzi* (Perlodidae), *Brachyptera seticornis* (Taeniopterygidae), *Leuctra hippopus* (Leuctridae) and even in *Capnia vidua* (Capniidae), a taxon with short and partly reduced wings (own observations). The muscle extends from the posterior part of the 1Ax to the pleural ridge. It might have been overlooked by WITTIG (1955) because it is obviously closely connected to tpm 49, which stretches between the lateral part of the notum and the pleural ridge.

MATSUDA (1970: 63) homologised the tpm 49 sensu WITTIG (1955) with t-p 15 of other Pterygota, which is stretched between the middle of the pleural ridge and the posterior notal wing process. The tpm 49 however, is not stretched between the PNP and the pleural ridge but rather between the lateral part of the scutum (anterior to the PNP) and the pleural ridge. In the examined Plecoptera it is a bipartite muscle, and only the first part of the muscle (tpm 49a), which is stretched between the scutum and the pleurum, is homologous to t-p 12.

The close connection between the axillary muscle (tpm 49b following this contribution) and the muscle tpm 49 (sensu WITTIG 1955) in Plecoptera suggests that the axillary muscle originated from tpm 49. In other neopteran taxa both muscles are well separated from each other, so the condition of Plecoptera could be interpreted as rather primitive.

In basal Ephemeroptera, the **1Ax** is provided with two muscles (for homology of axillaries see section 4.2.5). The first muscle is ventrally attached to the pleurum (Ax.PmI) and the second one runs to the furca (Ax.Fm). According to MATSUDA (1970), the **Ax.Fm** (t-s 3 of this author) is a primitive character and homologous with the muscle 45 of *Lepisma* sp. (Zygentoma). Among adult Pterygota, it has been retained only in Ephemeroptera (Figs. 36, 53–55, 101, 102; t-s 3 in Figs. 119–122). Furthermore, MATSUDA (1970: 65) wrote that Ax.Fm (t-s 3) connects the tip of the furca and the first (s1) or second axillary sclerite (s2) in Ephemeroptera. But in none of the examined taxa Ax.Fm is attached to the sclerite that is assumed to be the 1Ax (s1) by MATSUDA. Nevertheless, the Ax.Fm is not attached to the 1Ax (s2) in several Ephemeroptera. In *Baetis* sp. and *Cloeon dipterum* (Baetidae), for example, Ax.Fm is stretched between the proximal part of the basal plate (p in Figs. 27–29) and the furca (own observation). The changes could be correlated with the miniaturisation of the body size in Baetidae. The 1Ax (s2) is not clearly distinguish-

able in the wing base of those taxa. I consider both the fusion of the 1Ax with BP or the miniaturisation of 1Ax possible. In the first case, Ax.Fm is attached to 1Ax, which is fused to BP. Given the latter possibility, the attachment of Ax.Fm has been shifted onto the BP. In *Ephoron virgo* (Polymitarcyidae) the Ax.Fm is a relatively large muscle that inserts on the anterior part of the PNP (Fig. 40). In *O. rhenana* (Oligoneuriidae) Ax.Fm is absent. The latter two taxa are characterised by a swarming behaviour where the nuptial dances take place in form of a rapid horizontal flight (Brodsky 1973). Brodsky (1974) mentioned that Ax.Fm is reduced in Oligoneuriidae, which are characterised by the most modified flight behaviour. But the Ax.Fm is still present as a relatively large muscle in *Ephoron virgo* and according to Brodsky (1974) it is also present in *Palingenia longicauda* (Palingeniidae). These two taxa are characterised by a flight behaviour resembling that of Oligoneuriidae.

In Ephemeroptera, there is a second muscle associated with the 1Ax, the **Ax.PmI**. It is a narrow muscle that is ventrally attached to the pleurum. The anterior part of tpm 49 (tpm 49b), which attaches to the 1Ax in Plecoptera (see above), is homologised with the Ax.PmI of Ephemeroptera in this work. The shape of the muscle, not flat and broad but slender and almost round in cross section, is most likely an apomorphic condition in Ephemeroptera. Matsuda (1970) assumed a homology of Ax.PmI to t-p 13, which is a muscle stretching between the 3Ax and the episternum in Neoptera. This assumption is obsolete because his homology of the axillary sclerites of Ephemeroptera to that of Neoptera is not correct (see section 4.2). According to Matsuda, the Ax.PmI is shifted from the 3Ax to the 2Ax (homology of 2Ax and 3Ax following Matsuda 1956, 1970). Given the fact that Ax.PmI is not associated with the 3Ax but rather to the 1Ax, the Ax.PmI of Ephemeroptera is most likely the homologous muscle to t-p 11. The latter muscle stretches between the dorsal part of the pleural ridge and the 1Ax in other insects.

According to Matsuda's (1970) description of t-p 11, the anterior part of tpm 49 (sensu Wittig 1955) and the Ax.PmI (sensu Kluge 1994) are homologous with t-p 11 (sensu Matsuda 1970).

The muscle t-p 11 (pleurum –1Ax) is assumed to be a "more dorsally located t-p 10 [pleural arm–ANP]" (Matsuda 1970: 63), the t-p 10 again is supposed to be a derivate of t-p 12 (pleural arm–lateral scutum between ANP and PNP), which reflects the close relationships of these three muscles. The condition of Plecoptera suggests, that the muscle running from the 1Ax to the pleurum originates from the tergo-pleural muscle tpm 49 (sensu Wittig 1955, t-p 11 [or rather t-p 10] sensu Matsuda 1970).

Furthermore, Matsuda (1970) mentioned that t-p 15 occurs in Ephemeroptera and Plecoptera and that it is a modified t-p 14 in Ephemeroptera. In my view it is likely that t-p 14 and t-p 15 of Ephemeroptera (sensu Matsuda 1970) are not two different muscles but rather only one (the same) muscle. In several contributions there is only one muscle, lying in this area described. According to the same paper of Matsuda t-p 13, t-p 14 and t-p 15 are present in Ephemeroptera. The citations (Matsuda 1956, Knox 1935, Maki 1938) are inconsistent since each of the problematic muscles is cited only once (t-p 5, 6, for instance, is equivalent to muscle 43 sensu Matsuda 1956, Dvm 1 sensu Knox 1935 and also to muscle 25 sensu Maki 1935). The muscle t-p 14 is equivalent to 32 sensu Maki (1935) and not mentioned by Knox (1935) or Matsuda (1956), likewise the t-p 15 that is only mentioned in the work of Knox (II Pm 6 sensu Knox 1935) but not in the two other papers.

The t-p 13 of Ephemeroptera sensu Matsuda (1970) is certainly not the homologous muscle to the wing flexor (t-p 13) of other insects but rather t-p 11 (see above) since it is attached to the 1Ax (see section 4.2) in Ephemeroptera. Nevertheless, a muscle that is homologous with one of the neopteran wing flexor muscles (t-p 14) is present in Ephemeroptera (see below). This muscle is probably the II Pm 6 sensu Knox (1935; not pictured by her) and the muscle 32 sensu Maki (1938). Matsuda (1970), however, homologised the II Pm 6 with t-p 15, i. e. a muscle running to the PNP. This hypothesis is not correct and a muscle t-p 15 is not present in Ephemeroptera. The muscle 32 sensu Maki (1935), t-p 14 sensu Matsuda (1970) and II Pm 6 sensu Knox (1935; according to Matsuda 1970 equivalent to his t-p 15) are the same muscle namely t-p 14, which is stretched between the 3Ax and the epimeron next to the PWP.

The **3Ax** is most likely the dorsal attachment of two muscles in the ground plan of Neoptera. According to Brodsky (1994), only one muscle is present in insects that show a flat wing folding at rest. In those groups with a roof-like wing position at rest (and also in Diptera), both muscles (t-p 13 and t-p 14) occur (Brodsky 1994).

Only one axillary-pleural muscle is described in *Perla abdominalis* (tpm 48 sensu Wittig 1955). It is a rather long muscle that stretches between the 3Ax and the episternum. The homologous muscle to tpm 48 (Wittig 1955) is t-p 13 in other insects (sensu Matsuda 1970). Nevertheless, in all of the Plecoptera, which I have dissected, there are two muscles attached to the 3Ax. The first of these two muscles is short and ventrally attached to the pleurum next to the PWP (tpm 48b in Figs. 82, 83; t-p 14 sensu Matsuda 1970). The second muscle of the 3Ax is located adjacent to the first one and runs to the episternum next to the pleural ridge (tpm 48a in Figs. 82, 83; t-p 13 sensu Matsuda 1970). Most likely Brodsky (1994, e. g. in fig. 7.1 on p. 117) had mistaken t-p 14 for t-p 13 (sensu Matsuda 1970).

The 3Ax (for homologisation of the axillaries see sec-

tion 4.2) of Ephemeroptera and Odonata is equipped with a short muscle (**Ax.PmS**, muscles 29 and 30) running to the epimeron adjacent to the PWP. At least in some Ephemeroptera (e. g. *E. virgo*) as well as in Odonata it is bipartite. The second, shorter and much weaker part of Ax.PmS of Ephemeroptera is attached to the posterior part of the basal plate instead of the pleurum. It is likely a secondary development in this taxon. In Odonata both muscles (29 and 30) are only short. They take a parallel course and are both attached to the pleurum next to the PWP. While the presence of t-p 14 is a ground plan character of Pterygota, t-p 13 is an autapomorphic character of Neoptera.

Matsuda (1970) assumed that t-p 13 as well as t-p 14 is present in Ephemeroptera but his t-p 13 is attached to 1Ax (Ax.PmI sensu Kluge 1994, see above) in Ephemeroptera. Therefore, it has to be homologised with t-p 11.

Moreover, Matsuda (1970) confused the homologisation of the muscle that attaches to the 3Ax in Odonata. According to Matsuda (1970: 400), muscles 29 and 30 sensu Asahina (1954) are possibly homologous with t-p 14. Under remark 5 (concerning his "t-p 14?") he mentioned that these "... muscles are M. gubernator analis 1a, b of Tannert 1958 ..." (Matsuda 1970: 401). In contrast, he (Matsuda 1970: 64) further mentioned that t-p 26 of Odonata is homologous with "M. gubernator analis 1a, b of Tannert 1958" and also to muscle 31 sensu Maloeuf (1935) and Asahina (1954). On the same page Matsuda wrote that this muscle arises from the posterior surface of the pleural wing process and inserts on the proximal part of the anal vein in the axillary plate. This interpretation is not correct and comprehends two different muscles. According to Maloeuf (1935) the muscle 31 is not present in adult Odonata. Asahina (1954), in contrast, suggests that it occurs in *Epiophlebia superstes* (Anisozygoptera), *Davidius nanus* (Anisoptera) and *Mnais strigata* (Zygoptera). In *Sympetrum* cf. *striolatum* (Anisoptera) the muscle 31 is absent according to own observations. Nevertheless, given Asahina's (1954: 50) description the muscle 31 is attached to the end of lateral branch of the scutellum and to the upper portion of the intrapleural ridge, which is completely different to Matsuda's (1970) description of t-p 26. However, the description of t-p 26 (following Matsuda 1970) is consistent with the description of muscles 29 and 30 (sensu Asahina 1954). Consequently, the muscles 29 and 30 (sensu Asahina 1954) and M. gubernator analis (sensu Tannert 1958) as well as Ax.PmS (sensu Kluge 1994) and t-p 14 (sensu Matsuda 1970) are all the same (homologous) muscle.

4.3.7 Muscles of the pleural wing sclerites

Ephemeroptera and Plecoptera show different conditions concerning the attachments of the basalar and the subalar muscles as well as the location and the appearance of the associated sclerites, the basalare and the subalare.

The basalare of Plecoptera (BA in Figs. 123, 124) is provided with two muscles, the basalar-trochanteral muscle (M. basalare-endocoxalis, cpm 50 sensu Wittig 1955 and Zwick 1973) and the basalar-coxal muscle (M. basalare coxalis, cpm 51 of Wittig 1955 and Zwick 1973). The subalare of Plecoptera is the dorsal point of attachment of one usually large muscle running to the coxa (cpm 53, M. subalar-coxalis sensu Wittig 1955 and Zwick 1973; t-cx 8 sensu Matsuda 1970). In some species, a second muscle is present, running from a smaller sclerite that lies posterior to the subalare of the pleurum (ppm 56 in Fig. 125). Both muscles occur in all Plecoptera examined.

In most cases the so-called basalare of Ephemeroptera is detached from the episternum situated at the anterior base of the wing margin (BA in Figs. 4–8, 32, 33, 96). This crescent-shaped sclerite is the dorsal attachment of two muscles. In *E. virgo* (Polymitarcyidae), the crescent-shaped sclerite is secondarily attached to the episternum. The subalare (SA in Figs. 4, 10, 30–33, 43, 44, 93, 96, 97) in Ephemeroptera is provided with two muscles running to the sternum and one pleural muscle running to the coxal rim (SA.Sm, SA.Fm and SA.Cm; Figs. 14–19, 37, 50–55, 103–105, 110, 113–116). Subalar-sternal muscles are not present in Plecoptera or other Neoptera (Matsuda 1970). In Plecoptera, each of the two basalar muscles is about equal in proportion to the subalar-coxal muscle. In contrast, the subalar-sternal muscle of Ephemeroptera is considerably larger than the remaining basalar and subalar muscles.

Basalare and associated muscles

The basalare of Neoptera is most likely a pleural element (Snodgrass 1935), and in basal Pterygota it is even still associated with the pleurum. In all examined Plecoptera it is still connected to the episternum. The basalare of Plecoptera articulates anteriorly with the basicostale and posteriorly with the basisubcostale.

The interpretation of the basalare and its associated muscles in Ephemeroptera is problematic. Therefore, a homologisation with the basalare of Neoptera is difficult. The crescent-shaped sclerite lying basal to the tegula in Ephemeroptera is generally considered as basalare. Its upper part is tightly connected with the tegula. The crescent-shaped sclerite is neither connected directly to the base of the subcostal vein (Brodsky 1994) nor does it lie below the ANP (Hörnschemeyer 1998) as the basalare in Neoptera.

The two basalar-sternal muscles (BA.SmS, BA.SmI) of Ephemeroptera are attached to this crescent-shaped sclerite but the so-called basalar-coxal muscle (BA.Cm sensu Kluge 1994, 2004) and the so-called basalar-pleural muscle (BA.Pm sensu Kluge 1994, 2004) are not attached to it. The latter two muscles rather insert on two sclerites lying in the membrane between the notum and the anterior part of the wing base. BA.Pm usually inserts on a dorsal

sclerite that lies proximal to the crescent-shaped sclerite (Figs. 12, 40), almost at the same level as the anterior wing base (Fig. 12). Posterior to the insertion of BA.Pm and just anterior to s1 (ANP following the present study) lies the sclerite, at which BA.Cm inserts (Figs. 11, 12, 40). In some mayflies (e.g. *Baetis* sp., *Rhithrogena semicolorata*, *Ecdyonurus submontanus*) these sclerites are associated with each other, and additionally also connected to the crescent-shaped sclerite and the tegula (own observations). In other taxa (e.g. *E. virgo*; Fig. 40), these sclerites lie separated from each other in the anterior part of the wing base. BA.Cm is attached to the coxo-pleural joint and runs (directly below the s1) to the sclerite lying anterior to s1.

I could not verify the basalar-trochanteral muscle (**BA.Trm**), which is described in *Hexagenia* (Ephemeridae) by Knox (1935) and also in *Ephemerella* sp. (Ephemerellidae), *Ephemera* sp. (Ephemeridae), *Ecdyonurus* sp. (Heptageniidae), *Choroterpes* sp., *Habrophlebia* sp. (Leptophlebiidae), several Baetidae, *Oligoneuriella* sp. (Oligoneuriidae) and *Caenis* sp. (Caenidae) by Grandi (1947). On the other hand, Matsuda (1956) states that this muscle (t-tr 2 sensu Matsuda 1970) is not present in *Siphlonurus columbianus*, whereas he later (Matsuda 1970: 75) asserts that it is attached to the first axillary sclerite in other Ephemeroptera, very close to the point of attachment of t-cx 4 (BA.Cm sensu Kluge 1994). Matsuda's assumption that t-tr 2 is attached to the axillary sclerite resulted from Grandi's (1947) interpretation who described a muscle that is dorsally attached to the 1Ax (1Ax sensu Grandi). The dorsal point of attachment of t-tr 2 is close to that of t-cx 4 or fused with it (Matsuda 1970). According to the same author this muscle (t-cx 4) is described only in Ephemeroptera. Another trochanteral muscle is listed for the ephemeropteran thorax by Matsuda (p-tr 2 sensu Matsuda 1970: 124). It is the basalar-trochanteral muscle, which also occurs in Neoptera. The two muscles t-tr 2 and p-tr 2 are one and the same muscle in Ephemeroptera. But the first mentioned muscle is described as a tergal muscle by Grandi (1947), assuming that it inserts on the 1Ax. The second muscle is described as a pleural muscle by Knox (1935). According to Knox (II Pm 3 of this author) it is attached to the basalare, which is known as a pleural element in Neoptera. But if the two mentioned muscles are associated with t-cx 4, then the dorsal attachment of both t-tr 2 and p-tr 2 is the posterior sclerite lying antero-medial of s1 in the ephemeropteran wing base. Kluge (1994) mentioned a muscle BA.Trm in the list of abbreviations but he neither pictured nor mentioned the muscle in a later publication (Kluge 2004). Furthermore, a basalar-trochanteral muscle is pictured in Brodsky's diagram of the muscles of a generalised ephemeropteran mesothorax (Brodsky 1974: 38, fig. 2) with the same insertion as that of TCxm5 (classified as a basalar-coxal muscle, BA.Cm). He described the function of this muscle as pronator of the wing. In spite of this, he marked the TTrm2 as absent in the mesothorax of all Ephemeroptera examined (Brodsky 1974: 38, tab. 1).

The scuto-trochanteral muscle (S.Trm) is attached to the lateral part of the scutum in larval Ephemeroptera (own observation). It seems to have been shifted more laterally in subimaginal and imaginal Ephemeroptera compared to its position in the larvae. Though, it is a large muscle in larvae it is diminished in the winged stages. Its lateral position and the size of S.Trm probably cause misinterpretations. Nevertheless, in none of the examined taxa a basalar-trochanteral muscle was found.

The basalar-sternal muscles (**BA.SmS**, **BA.SmI**; p-s 12 sensu Matsuda 1970; Figs. 14–19, 50–54, 98, 111; p-s 12 in Figs. 118–121) that are present in Ephemeroptera are absent in the mesothorax as well as in the metathorax of Plecoptera and the remaining Neoptera (Matsuda 1970). They are most likely reduced in these taxa. There are two muscles in the thorax of Lepismatidae, which lie in exactly the same position as the ephemeropteran BA.SmS and the BA.SmI (muscles 41 and 42 sensu Barlet 1953, 1954 and Matsuda 1970). This was the reason for Matsuda to assume a homology of the lepismatid muscles 41 and 42 with the basalar-sternal muscles in Ephemeroptera. Both muscles (41 and 42) of *Lepisma saccharina* (Zygentoma) are tergosternal muscles. Matsuda (1970) interpreted them as pleuro-sternal muscles, most likely because the basalare is generally known as a pleural element in other Pterygota. However, in Ephemeroptera all of the so-called basalar muscles are of tergal origin. Matsuda (1970: 120) also assumed – without reasoning – that the p-s 12 is shared only by Ephemeroptera and Odonata, but nevertheless omits these muscles elsewhere (Matsuda 1970: 400, tab. XXIV). Matsuda also wrote in this publication that a different muscle is present (t-s 2), which originates on the midlateral portion of the mesothoracic prescutum and inserts at the postero-dorsal surface of the prothoracic furca. According to (Matsuda 1970: 65) it is probably homologous with muscle 42 of *Lepisma* sp., which in turn is homologised with p-s 12 (BA.SmS/BA.SmI sensu Kluge 1994).

Muscle t-s 2 should also occur in larval stages of *Corydalus* sp. (Megaloptera) and in *Stagmomantis* sp. (Mantodea). Another muscle p-s 3, which is stretched between the episternum and furca of the preceding segment, occurs in Psocoptera, Hymenoptera, Coleoptera and Lepidoptera and is assumed to be a derivate of p-s 12. On the above mentioned assumptions, it is not feasible that p-s 12 is a synapomorphic character of Odonata and Ephemeroptera as assumed by Matsuda (1970). In the examined Plecoptera, however, no homologous muscles to BA.SmS and BA.SmI of Ephemeroptera were found. In my view, BA.SmS and BA.SmI are plesiomorphic ground plan characters of Pterygota, as these muscles are already present in Zygentoma (Barlet 1953, 1954). Consequently these mus-

cles must be interpreted as symplesiomorphic in Ephemeroptera and Odonata. Both muscles are likely to be reduced in Neoptera.

Brodsky (1970: 166) mentioned that the basalare of Ephemeroptera "occupies its usual place" Assuming that the basalare is, just as well as the neopteran basalare, a pleural element, he classified all basalar muscles of Ephemeroptera as pleural muscles (Pm). Four years later (with reference to Matsuda 1970, see above) and on the grounds that the homologous muscles are associated with the tergum in *Lepisma saccharina* and not present in any other insect order, he termed the basalar-sternal muscles TSm1, tergo-sternal muscles (Brodsky 1974). Interestingly, he also interpreted the BA.Cm (TCxm5) and the BA.Pm (TPm3) as tergal muscles in the latter publication. In larval mayflies, the two mentioned basalar-sternal muscles are indeed dorsally attached to the anterior part of the scutum (see Fig. 56).

In the pterothorax of Odonata there are two muscles present, which are connected to the lateral part of the humeral plate (hp) by a long tendon (muscles 21 and 22 sensu Maloeuf 1935 and Asahina 1954; Figs. 59, 61–63, 65, 66). Matsuda (1970) suggested that both muscles are autapomorphic characters of Odonata (t-p 22 and t-p 23 sensu Matsuda 1970). In the same contribution (on p. 120) however, he wrote that p-s 12 is shared by Ephemeroptera and Odonata without any further reasoning. In my view, p-s 12 is indeed present in Ephemeroptera (BA.SmS and BA.SmI sensu Kluge 1994) and Odonata (muscles 21 and 22 sensu Asahina 1954).

The muscle 22 has a bipartite dorsal tendon that inserts in addition to the lateral attachment also to the middle part of the hp. Muscles 21 and 22 are interpreted as sternobasalar muscles by Asahina (1954) though they are attached to the pre-episternal sclerite sensu Asahina. Actually the characteristics of muscles 21 and 22 when compared to BA.SmS and BA.SmI of Ephemeroptera are nearly identical. In both taxa, these muscles are attached to a sclerite close to the anterior wing base. Asahina assumed in the same paper that the hp of Odonata contains a part of the basalare. Interestingly, Brodsky (1994) homologised at least a part of the hp of Odonata with the basalare, but without any reasoning. I agree with Brodsky's and Asahina's assumption since the position of the hp in Odonata is comparable with the position of the crescent-shaped sclerite in Ephemeroptera. Moreover, in Odonata two muscles are attached to the hp just in a similar position as BA.SmS and BA.SmI of the so-called basalare in Ephemeroptera. This makes it likely that BA.SmS and BA.SmI of Ephemeroptera are homologous with the muscles 21 and 22 of Odonata. The so-called basalar sclerites of Ephemeroptera and Odonata are most likely not homologous to the basalare of Neoptera. Comparing the musculature of Zygentoma (Barlet 1953), Ephemeroptera and Odonata it becomes obvious that a reduction of the basalar-sternal muscles is an apomorphic character of Neoptera rather than a synapomorphic character of Metapterygota as assumed by Willkommen & Hörnschemeyer (2007).

In Ephemeroptera there is also a so-called basalar-pleural muscle (**BA.Pm**; Figs. 12, 18, 19, 40, 52–55, 99; t-p 4 in Fig. 122) present. It is dorsally attached to the sclerite lying proximal to the anterior wing base and to the crescent-shaped sclerite. From there it proceeds to the pleurum (Fig. 32). In some of the examined species (*Baetis* sp., *Rhithrogena semicolorata*, *Ecdyonurus submontanus*) this sclerite is associated with the crescent-shaped sclerite (own observation). The BA.Pm (sensu Kluge 1994) of Ephemeroptera is similar to p5 sensu Matsuda (1970) and m. pleurocondilo-scutale sensu Grandi (1947). According to Matsuda (1970) BA.Pm is only present in Ephemeroptera stretching between the BA and PWP.

Such a short but robust muscle lying in the same position is also present in Plecoptera (tpm 47 sensu Wittig 1955; Fig. 83) and also in Odonata (own observation, see Figs. 64, 65). In *Pteronarcys reticulata* (Pteronarcyidae), *Perla abdominalis* (Wittig 1955) and also in *Isoperla grammatica*, *Isoperla goertzi*, *Perlodes microcephalus* (Perlodidae), *Capnia vidua* (Capniidae, all Plecoptera; own observations) it inserts dorsally on a small sclerite next to the tegula (Fig. 67), i. e. the subtegula (Snodgrass 1935, "kleine Sklerifikation hinter der Tegula" sensu Wittig 1955, "myodiscus" sensu Nelson & Hansson 1971). This muscle proceeds to the episternum, namely anterior to the PWP. Though tpm 47 is conspicuous in *Brachyptera seticornis* (Taeniopterygidae), this sclerite is rather indistinct.

In Odonata the short muscle 28 (Asahina 1954) has a similar course, as it is also dorsally attached to a tergal sclerite and running to the pleurum anterior to the PWP. Matsuda (1970: 401) homologised muscle 28 of Odonata with t-p 11, which connects the anterior (or dorsal) part of the pleural ridge or the anterior part of the PWP with the first axillary sclerite in other insects. This assumption may result from Tannert's interpretation of the dorsal sclerite, to which muscle 28 is attached, as 1Ax (Pt 1 sensu Tannert 1958). The first axillary sclerite, however, is expected to be located rather posterior to this sclerite when compared to the wing base of the remaining Pterygota. It should be rather located proximal to the axillary plate since the characteristics of the axillary plate suggest homology to at least a part of the wing base sclerites (2Ax, 3Ax and PMP) of other Pterygota (see section 4.2).

The muscle 28 (metathoracic muscle 50 respectively; Fig. 65) that is attached to this sclerite in Odonata is similar to BA.Pm of Ephemeroptera and to t-p 4 of the Neoptera. The t-p 4 originates from the pleural ridge just below the pleural wing process or – if developed – from the pleural

arm (MATSUDA 1970: 62). It inserts either at the subtegula, the laterophragma, or the prealar sclerite. MATSUDA (1970: 15) also assumed that the sclerite, to which the t-p 4 is dorsally attached in Neoptera, is presumably a detached prescutal sclerite. The BA.Pm of *Siphlonurus aestivalis* (Siphlonuridae) is attached to a sclerite lying between the tegula and the tergum. This sclerite is also associated with the posterior arc of the prealar bridge. This is indeed an indication of the prescutal origin of the sclerite and supports ASAHINA's assumption, that the sclerite, which is located proximal to the humeral plate in Odonata (Pt 1 following TANNERT 1958), is a part of the prescutum (ASAHINA 1954).

In mayfly larvae, the muscle BA.Pm is dorsally attached to the latero-medial part of the scutum. Regarding the similar attachment of this short muscle in Ephemeroptera (BA.Pm sensu KLUGE 1994), Odonata (muscle 28 sensu MALOEUF 1935), Plecoptera, and other Neoptera (t-p 4 sensu MATSUDA 1970) it is most likely that BA.Pm, muscle 28 and muscle t-p 4 are homologous with each other.

Consequently, the BA.Pm of Ephemeroptera is not a genuine basalar muscle but rather the muscle running from the subtegula to the pleurum (t-p 4). Therefore, the sclerite to which the muscle is attached is not the basalare but rather the subtegula.

In Ephemeroptera the dorsal attachment of **BA.Cm** (Figs. 12, 40) is behind that of BA.Pm. In Plecoptera and also in other Neoptera there is a basalar-coxal muscle (basalar-coxal or M. basalare coxalis, cpm 51 sensu WITTIG 1955 and ZWICK 1973), which pronates the wing. It is dorsally attached to the episternal basalare and ventrally to the anterior rim of the coxa (Fig. 82).

In contrast, the basalar-coxal muscle (BA.Cm sensu KLUGE 1994) of Ephemeroptera is often interpreted as a coxo-axillary or coxo-tergal muscle. MATSUDA (1956, 1970) assumed that the muscle is dorsally attached to the 1Ax (s1: 1Ax sensu MATSUDA 1956 and TSUI & PETERS 1972, pseudopterale prossimale sensu GRANDI 1947; s1 see also section 4.2.5). BRODSKY (1974) termed this muscle as a tergo-coxal muscle (TCxm5, see above) and KLUGE (1994) interpreted it as a basalar-coxal muscle.

In nearly all examined mayflies (in particular in *Siphlonurus aestivalis*), the dorsal attachment of this so-called basalar-coxal muscle is on the dorsal sclerite next to the s1 (own observation; Fig. 11). In *S. columbianus*, examined by MATSUDA (1956), the muscle is interpreted as axillary muscle. However, in *Habroleptoides confusa* (Leptophlebiidae), *Centroptilum luteolum* and *Cloeon dipterum* (Baetidae) there is a different configuration present (own observation). In addition to the usual attachment of BA.Cm in *H. confusa* there is an indistinct tendon running to s1. In *C. luteolum* the muscle is dorsally attached to an antero-proximal projection of the basal plate. In *Cloeon dipterum* the BA.Cm is attached to the conspicuous base of the subcostal vein. These character states in Baetidae are likely correlated with the miniaturisation of the body size and the changes in wing base sclerites.

MATSUDA (1970) assumed that the t-cx 4 (BA.Cm) is a direct flight muscle of Ephemeroptera and Odonata. Furthermore, in *Siphlonurus* it is supposed to insert at the 2Ax (s2; axillary homologisation following MATSUDA 1970). However, in *Siphlonurus columbianus* (muscle 50 sensu MATSUDA 1956) and in *Ecdyonurus* (Heptageniidae) it is assumed to insert at the 1Ax (s1; axillary homologisation following MATSUDA 1956, 1970). According to KNOX (1935), the BA.Cm is dorsally attached to the basalare. This is due to the fact that in several mayflies the sclerite, which is the dorsal attachment of BA.Cm, is connected to the crescent-shaped sclerite (so-called basalare, BA). The large sclerite figured in KNOX's (1935: 137) plate XX is most likely this crescent-shaped sclerite plus the tegula plus the associated dorsal sclerites (attachment of BA.Pm and BA.Cm). In several species, these elements are tightly connected to each other (see above). Nevertheless, the muscle (BA.Cm) is not associated with the 1Ax (2Ax following MATSUDA 1956, 1970) and in most cases also not with s1 (1Ax following MATSUDA 1956, 1970) in the examined Ephemeroptera.

MATSUDA (1970: 66) assumed that in Odonata there are two muscles present, which connect the disc internal to the coxal condyle with the first axillary sclerite and the axillary plate (second and third axillary sclerites). Their ventral points of attachment are confluent and their dorsal attachments lie close to each other. Therefore, MATSUDA termed the muscles t-cx 4 and t-cx 4′ (assuming that t-cx 4 is homologous with BA.Cm of Ephemeroptera). These two muscles are 26 and 27 sensu MALOEUF (1935) and ASAHINA (1954).

The position of the muscle 27 of Odonata is different from the position of BA.Cm of Ephemeroptera. MAKI (1938) assumed that in addition to muscle 26 also muscle 27 is a coxo-axillary muscle, which is attached to the axillary plate of the wing base in Odonata. ASAHINA (1954: 45) assumed that it could be a coxo-subalar muscle, which is generally present in the other winged insects. The muscle 27 is dorsally attached to the axillary plate, which is likely partially fused with the subalare in Odonata (see below). As muscle 27 rather resembles a subalar muscle than a basalar-coxal muscle, this study agrees with the hypothesis of ASAHINA (1954).

Muscle 26 (Figs. 59, 65) of Odonata, however, is very similar to BA.Cm of Ephemeroptera regarding the dorsal and ventral attachment points. The dorsal attachment of muscle 26 is located proximal to the humeral plate, which is fused with the sclerite homologous with the crescent-shaped sclerite of Ephemeroptera. ASAHINA (1954: 45) wrote that it appears more reasonable to ascribe it to the coxo-basalar muscle. A homology of the muscle 26 of

Odonata with the BA.Cm of Ephemeroptera is also assumed in the present study. The so-called basalar-coxal muscle of Ephemeroptera and Odonata are possibly not homologous with the neopteran basalar-coxal muscle (see below).

The BA.Cm of Ephemeroptera is sometimes described as a basalar muscle (BA.Cm sensu Kluge 1994, Pm3 sensu Brodsky 1970). Nevertheless, all basalar muscles in mayfly larvae are dorsally attached to the antero-lateral or medio-lateral part of the scutum (Fig. 56). Their pleurum is rather simple and small. The pleural sclerite is separated from the tergum by a membranous area. In contrast, the pleurum of stonefly larvae is large and the upper part of the episternum is associated with the tergal parts. It lies next to the anterior wing base, whereas the epimeron is rather small. Between the posterior part of the epimeron and the ventral membrane of the wing pad there is a relatively large membranous area. So the dorsal attachment of the two basalar muscles on the episternum is next to the tergal parts in larvae of Plecoptera.

Most likely the small, isolated and simple pleurum of larval Ephemeroptera represents the plesiomorphic condition. The pleurum of larval Plecoptera is closely associated with the tergum, which probably represents a derived state. One possible interpretation is the assumption that the basalar muscles are of tergal origin in Pterygota. In Neoptera these muscles shifted ventrally onto the pleurum.

However, the BA.Cm is attached to a separate sclerite of the anterior wing base in Ephemeroptera. In subimagines, imagines and also in larvae of Ephemeroptera the attachment lies even posterior to the attachment of BA.Pm, which is not a genuine basalar muscle (see above). Therefore, it is more likely to assume that the BA.Cm of Ephemeroptera is also not a true basalar muscle. Therefore a homology of BA.Cm to the basalar-coxal muscle of Neoptera is rather unlikely, but a homology of BA.Cm of Ephemeroptera to the muscle 26 of Odonata is assumed. The sclerites, to which BA.Pm and BA.Cm are attached are separated in basal Ephemeroptera, which is likely to represent the plesiomorphic condition. Therefore, the term BAd (which includes the two sclerites) used by Willkommen & Hörnschemeyer (2007) is not correct, since the separated dorsal sclerites are not true basalar sclerites. The anterior sclerite, lying between the tegula and the tergum at the anterior wing base is homologous with the subtegula of other Pterygota (see above).

Subalare and associated muscles

In Plecoptera the subalare is a simple, longish sclerite without large apodemes, but conspicuous and specialised in the Ephemeroptera. In both Ephemeroptera and Plecoptera, the subalare develops from the pleural membrane below the wing pad. It is located in the upper part of the pleurum posterior to the PWP and below the wings. The sclerite is surrounded by a membranous area in both taxa and never associated with the epimeron.

The subalar-coxal muscle (**SA.Cm**; Figs. 18, 19, 54, 55) of winged stages of Ephemeroptera is dorsally attached to the anterior subalar apodeme (ASA; Figs. 4–8 10, 43, 96) and ventrally to the postero-lateral rim of the coxa. Usually, it is a rather weak and sometimes bipartite muscle in imaginal Ephemeroptera. The large subalar-sternal muscle (SA.Sm; Figs. 14–17, 37, 50–53, 103–105, 110, 113–116; t-cx 8 in Figs. 117–120) is attached to the posterior subalar apodeme (PSA; Figs. 4–8, 10, 17, 18, 30, 32, 33, 43, 44, 104, 114, 115) and to the subalar suture (SAs; Figs. 8, 30, 32, 33). The SA.Sm originates from the furcasternite (FS; Figs. 4, 5, 34, 44, 48, 109).

In the larval stages of Ephemeroptera, the pleurum is rather simple and small. The SA.Cm inserts at the postero-dorsal part of the pleural sclerite next to the pleural suture (Fig. 56). It originates from the lateral rim of the coxa. In contrast, the SA.Sm is attached to a small sclerite in the upper part of the pleural membrane directly below the posterior part of the fore wing pad (Fig. 56). The subalar-furcal muscle (SA.Fm) inserts at the same sclerite and originates from the mesothoracic furca.

In Neoptera, the subalare is provided with a large muscle running to the posterior rim of the coxa (subalar-coxal muscle; t-cx 8 sensu Matsuda 1970, cpm 53 sensu Wittig 1955 and Zwick 1973). In early stages of stonefly larvae (*Perla abdominalis*, Wittig 1955), the subalar-coxal muscle is stretched between the upper part of the pleural membrane near the future ventral membrane of the wing pad and runs to the rim of the coxa. Furthermore, it is attached to a small sclerite below the wing pad in final larval stages (e. g. *Brachyptera seticornis*).

Matsuda (1970) homologised the t-cx 8 (SA.Cm) of Ephemeroptera with the t-cx 8 of Plecoptera. However, in my opinion the SA.Cm of Ephemeroptera is most likely not homologous with the subalar-coxal muscle of Plecoptera and other Neoptera because the origin of this muscle in larval stages is different in Ephemeroptera and Plecoptera. The anterior part of the subalare, which is equipped with the anterior subalar apodeme (ASA) in Ephemeroptera is either secondarily associated with the posterior part of the subalare, or the dorsal attachment of SA.Cm has shifted onto the subalare in the winged stages. The posterior part of the SA of Ephemeroptera develops ontogenetically similar to the subalare of Plecoptera, namely below the wing pad and in the pleural membrane above the epimeron. In contrast, the anterior part of the subalare that provides the ASA may develop from the upper part of the pleurum. Later in its larval development it possibly becomes associated with the posterior sclerite of the subalare. This suggests that the anterior part of the subalare of Ephemeroptera is not homologous with the subalare of

Plecoptera and other Neoptera. A homology of the subalar-coxal muscle (SA.Cm) of Ephemeroptera to the subalar-coxal muscle (t-cx 8 sensu MATSUDA 1970) of Plecoptera and other Neoptera is rather unlikely.

MATSUDA (1970: 65) assumes that the **SA.Sm** of Ephemeroptera may be a derivative of the subalar-coxal muscle (t-cx 8), but does not mention any possible homologous muscle in *Lepisma saccharina* or *Lepismachilis* sp. (Zygentoma). The similar course of the SA.Sm in the larvae of Ephemeroptera compared to the SA.Cm in Plecoptera implies that MATSUDA's hypothesis concerning the origin of the SA.Sm is most probably correct.

It is difficult to decide whether the sternal attachment of the subalar muscle in Ephemeroptera could reflect a primitive or a derived condition. Nevertheless, the Ephemeroptera are characterised by a specialisation of the mesothorax that includes the enlargement of the indirect flight musculature (e. g. dorsal longitudinal muscle and some of the dorso-ventral muscles; see sections 4.2–4.4), the shortening of the metathorax and hind wings, and the coupling of fore and hind wings in flight. The above mentioned facts rather suggest that the enlarged SA.Sm of Ephemeroptera, in comparison to the conditions of the subalar-coxal muscle of Plecoptera, is a specialised homologue of the SA.Cm of Neoptera. MATSUDA (1970) assumed a homology of SA.Cm in Pterygota to a tergo-coxal muscle (62 sensu MATSUDA 1970) in *L. saccharina*.

Assuming that the SA.Sm is a specialised subalar-coxal muscle, one can also hypothesise that the subalar-furcal muscle (**SA.Fm**; t-s 4 sensu MATSUDA 1970) of Ephemeroptera is a split off from SA.Sm that evolved together with the specialisation of the subalare, since the SA.Fm is dorsally also attached to the PSA. Moreover, it is closely associated with the SA.Sm. A subalar-furcal muscle does not exist in the pterothorax of Plecoptera and other Neoptera. MATSUDA (1970) assumed that a subalar-furcal muscle is probably also present in certain Hymenoptera. A homology of SA.Fm to a muscle of *Lepismachilis* sp. or *Lepisma* sp. is not given by him. Assuming that SA.Fm is a specialised part of the SA.Sm it may also be homologous with muscle 62 (sensu MATSUDA 1970) of *L. saccharina*.

The homology of the subalar-sternal muscle (SA.Sm) and the subalar-furcal muscle (SA.Fm) of Ephemeroptera on the one hand to the subalar-coxal muscle (t-cx 8 sensu MATSUDA 1970) of Neoptera on the other hand is evident.

In Plecoptera there is a subalar-pleural muscle present, (ppm 56 sensu WITTIG 1955, t-p 16 sensu MATSUDA 1970), which extends between a small posterior sclerite (or the posterior part of the subalare; Fig. 125) and the ventral part of the epimeron. Such a muscle is not present in Ephemeroptera, but it occurs in lower Pterygota. Therefore, MATSUDA (1970) suggested a homology to a muscle of *Lepismachilis* (muscle 115 or 120 following MATSUDA 1970) that agrees approximately with the position of t-p 16. Consequently, the lack of a subalar-pleural muscle should be regarded as an apomorphic character of Ephemeroptera. MATSUDA (1970: 77, tab. 1) also considered the possibility of a new development in Pterygota. According to BRODSKY (1979b), the presence of the muscle t-p 16 can be attributed to the groundplan of Plecoptera. In my opinion this muscle is an apomorphic character of Metapterygota, and its absence in Ephemeroptera reflects the plesiomorphic condition.

At least three muscles are present in Odonata that could be homologised with subalar muscles. The muscles 32, 33 and 34 (sensu ASAHINA 1954) are dorsally associated with the ventral part of the axillary plate of the wing base (Figs. 62–65).

The first mentioned muscle (muscle 32) is the largest one. It is dorsally attached to the anterior part of the axillary plate by a tendon. According to MATSUDA (1970) this muscle (muscle 32; t-p 24 sensu MATSUDA 1970) is only present in Odonata. The dorsal point of attachment suggests that it is a subalar muscle since in larval Ephemeroptera, as well as in larval Plecoptera, the subalar muscles are attached to the pleural membrane immediately below the wing pad. The muscle 32 is probably the homologue of SA.Cm of Neoptera that shifted its ventral attachment as a result of a modification of the sternal and pleural elements. The ventral attachment is on the margin between katepisternum and epimeron (following ASAHINA 1954) next to the coxa.

Posterior to the muscle 32 are the dorsal points of attachment of the muscles 33 and 34. Both are rather small muscles that are attached to a small sclerite in the upper third of the membrane posterior to the pleural wing process. Each of the two muscles is also attached to the posterior part of the axillary plate, each by a tendon. According to MATSUDA (1970), both muscles (muscle 33 sensu ASAHINA 1954, t-p 25 sensu MATSUDA 1970; muscle 34 sensu ASAHINA 1954, and t-p 21 sensu MATSUDA 1970) are only present in Odonata. It would be conceivable that muscle 33 is either homologous with the subalar-coxal muscle as a separated and specialised part or rather, the homologue of the neopteran t-p 16. The latter assumption would be more parsimonious. Most likely the muscle 34 of Odonata is also the homologous part to t-p 16 (sensu MATSUDA 1970) of Neoptera. This assumption is supported by the fact that the subalare is located next to the ventral membrane of the wing pad and is fused with the axillary plate in Odonata as suggested also by ASAHINA (1954).

Furthermore, the attachment points of muscle 27 of Odonata suggest that it is most likely the homologous muscle to t-cx 8 of Neoptera. The dorsal attachment point is similar in both muscles 27 and 32. Thus, muscle 32 is probably a second, specialised part of the muscle 27.

MATSUDA (1970: 68f) hypothesised a tergal origin of

the subalar muscles (t-cx 8, t-p 16) since MAKI (1938) has shown that the future subalar-coxal muscle is dorsally attached to the lateral margin of the tergum in the late embryo of *Leucophaea* (Blattaria), or on the ventral base of the rudimentary wing in the early nymphal stages of *Locusta* (Orthoptera).

MATSUDA also wrote in the same paper that the number of prothoracic tergo-coxal muscles (where the subalare is missing) should be the same as in the pterothorax including the subalar-coxal muscle. According to him, this tendency ought to be recognisable in lower orders. He further stated (on p. 64) that in the nymph of *Perla*, according to WITTIG (1955), the subalar-pleural muscle (ppm 56, t-p 16) inserts on the posterior membrane near the area where the subalare (Flügelscheide) is later formed. WITTIG (1955), however, wrote that the muscle ppm 56 is attached to the posterior part of the pleural membrane.

The dorsal points of insertion of the subalar muscles in the examined larval mayflies and stoneflies (except the SA.Cm of Ephemeroptera) are close to the ventral membrane of the wing pads though never directly on the pterothoracic tergites. Therefore, a tergal origin of the subalar-coxal (and the respective subalar-sternal muscle of Ephemeroptera) and the subalare is conceivable but not obligatory. This assumption suggests that the wings are also of tergal origin and a duplication of the tergite.

In any case the musculature of *L. saccharina* has to be re-examined to assert the homologies of the subalar muscles and their basal precursors.

The dorsal point of attachment of SA.Cm in ephemeropteran larvae does not agree with the assumption of a tergal origin, since SA.Cm is attached to the pleural sclerite in ephemeropteran larvae (Fig. 56). It is probably even not homologous with the subalar-coxal muscle of Neoptera (see above).

In the metathorax of Ephemeroptera, the pleural sclerites and also the sternal elements are partly reduced or rather fused. Thus the subalar muscles of the metathorax are also reduced, and the furcasternum is either reduced or absent. In several Ephemeroptera both SA.Cm and SA.Sm are present and distinguishable in the metathorax. Both muscles are running close to each other, albeit the ventral attachment of the SA.Sm is on the coxa rather than on the furcasternite.

4.4 Sister group relationships (Figs. 126, 127)

General Remarks

There are three hypotheses on the basal splitting of Pterygota, namely the Chiastomyaria hypothesis, the Palaeoptera hypothesis and the Metapterygota hypothesis (BECHLY et al. 2001; BÖRNER 1909; BOUDREAUX 1979; FÜRST VON LIEVEN 2000; GORB et al. 2000; HENNIG 1953, 1969; HOVMÖLLER 2002; KRISTENSEN 1975, 1981, 1991; KUKALOVÁ-PECK 1978, 1983, 1985, 1991, 1998; LEMCHE 1940; MARTYNOV 1925; MATSUDA 1970; REHN 2003; SCHWANWITSCH 1943; SNODGRASS 1935; SOLDÁN 1997; STANICZEK 1996, 2000, 2001; WAGNER et al. 1996; WOOTTON 1979).

Chiastomyaria hypothesis

The Chiastomyaria hypothesis assumes a sister group relationship between Odonata and Ephemeroptera+Neoptera (LEMCHE 1940, SCHWANWITSCH 1943). This is based on different modes of wing pad development in both groups and also on the different development of the flight musculature. The first character is disputable because the wing pad development is inconsistent among Neoptera (HENNIG 1969, KUKALOVÁ-PECK 1978). In Odonata mainly the direct flight musculature is used, whereas in Ephemeroptera and Neoptera the indirect flight musculature is predominantly developed. A comparison with Zygentoma and Archaeognatha as outgroups implies that the direct flight musculature is an apomorphic feature of the Odonata. The indirect wing musculature is a ground plan character of Pterygota and therefore cannot be used as evidence for a sister group relationship between Ephemeroptera and Neoptera (PFAU 1986, KRISTENSEN 1981). Only the direct sperm transfer is a putative apomorphic character of Ephemeroptera and Neoptera, but also controversial because it is quite possible that the direct sperm transfer evolved convergently (BECHLY et al. 2001). In view of the large number of characters that support the Metapterygota or even the Palaeoptera hypothesis, a sister group relationship of Odonata to all other Pterygota is rather unlikely.

Palaeoptera hypothesis

The Palaeoptera hypothesis (MARTYNOV 1925) assumes that Ephemeroptera+Odonata is the sister group of Neoptera. The Palaeoptera are characterised by their inability to fold the wings horizontally over the abdomen (HENNIG 1969; KUKALOVÁ-PECK 1978, 1985; MARTYNOV 1925; WOOTTON 1979).

The proximate stem of the anterior and the posterior radial vein (R, Rs) are interpreted as plesiomorphic characters of the Palaeoptera. The fused medial stem is supposed to be the apomorphic condition shared by all Palaeoptera (including fossil taxa) (KUKALOVÁ-PECK & BRAUCKMANN 1990, KUKALOVÁ-PECK 1991). The common stem of the anterior cubital vein and the cubital sector as well as the intercalary veins are given as possible synapomorphic characters supporting the Palaeoptera hypothesis (KUKALOVÁ-PECK 1983, 1985, 1991, 1998; KUKALOVÁ-PECK & BRAUCKMANN 1990; RIEK & KUKALOVÁ-PECK 1984; STANICZEK 2001). Intercalary veins, however, are not present in the fossil odonatan taxon *Eugeropteron* (WILLMANN 2005). The common stem of the medial veins is probably a derived state. A basal fusion of the wing veins support rigid-

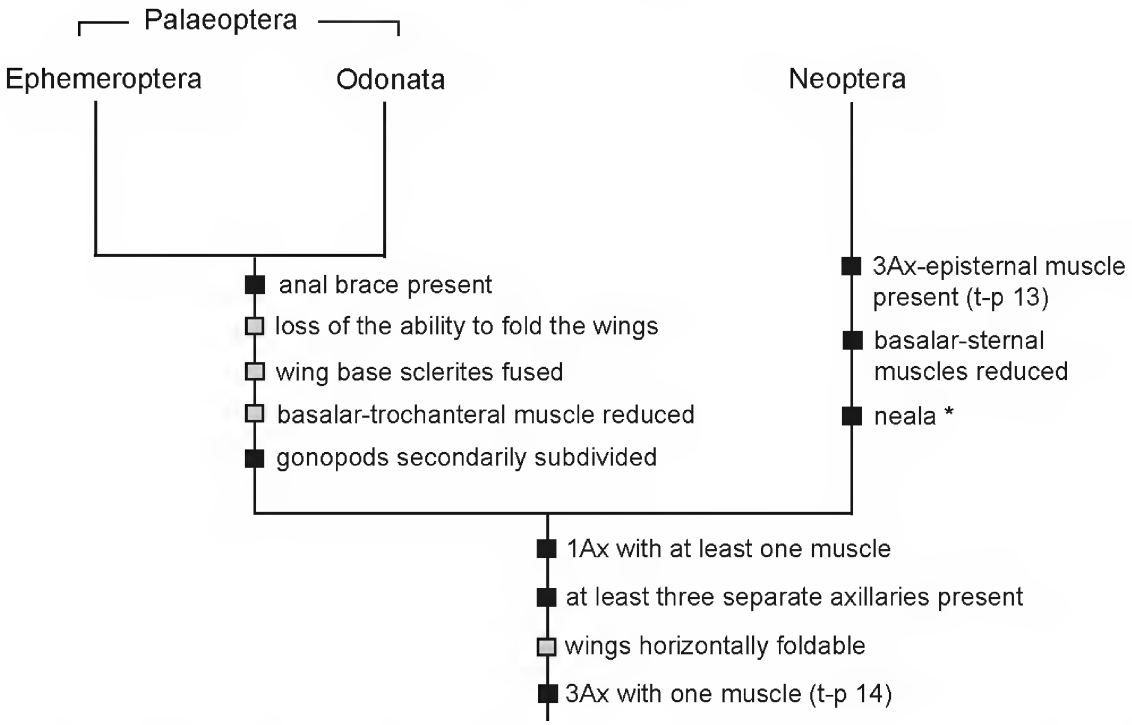

Fig. 126. Palaeoptera hypothesis, argumentation scheme of character evolution (modified after WILLKOMMEN & HÖRNSCHEMEYER 2007: fig. 24). – * = character after MARTYNOV (1925); grey box = uncertain character; for further interpretation see section 4.4.

ity at the wing base and therefore, it is difficult to exclude a convergent evolution of this character. WAGNER et al. (1996) regarded the imaginal microsculpture of ephemeropteran and odonatan wings as an autapomorphy of Palaeoptera. A similar microsculpture, however, also occurs in Neuroptera (WAGNER et al. 1996).

Nevertheless, it is problematic to take wing characters as apomorphies without the possibility to verify these characters in any of the basal outgroups.

The braces between the radial sector and the anterior medial vein (rp-ma), the brace between the medial vein and the cubitus (m-cu), and the brace between the posterior cubital veins and the anal vein (cup-aa1) are considered as synapomorphies of Palaeoptera (KUKALOVÁ-PECK 1998). Except of the cup-aa1 brace, in stem group representatives of Ephemeroptera and Odonata all other braces are either present as simple cross veins (*Bojophlebia*) or even absent (*Eugeropteron*) (STANICZEK 2001). So these characters obviously evolved convergently and cannot be interpreted as synapomorphies of Palaeoptera (STANICZEK 2001). Moreover, the costal brace is possibly an autapomorphic character of Ephemeroptera (WILLMANN 1999). A further synapomorphic character of the Palaeoptera could be the paired penes (BECHLY et al. 2001) but it may be also interpreted as a plesiomorphic character of the Insecta (see STANICZEK 2001).

The short antennae in Ephemeroptera and Odonata ("Subulicornia") evolved most likely convergently because long antennae were still present in *Namurotypus*, a stem group representative of Odonata (BECHLY et al. 2001, BRAUCKMANN & ZESSIN 1989).

The basalar-trochanteral muscle, which is present in Neoptera is absent in Ephemeroptera and Odonata. The assumption that the presence of this muscle is a ground plan character of Pterygota and the homologous structure to muscle 55 of *Lepisma* (MATSUDA 1970) suggests that it is secondarily reduced in Ephemeroptera and Odonata and supports the Palaeoptera hypothesis.

The paleopterous wing condition in Ephemeroptera and Odonata with their inability to fold the wings horizontally over the abdomen has been generally accepted as a symplesiomorphic character for a long time. Likewise, the presence of a wing flexor muscle in Neoptera is usually interpreted as derived character (MATSUDA 1970). This muscle running from the 3Ax to the pleurum allows the wing folding to a horizontal resting position over the abdomen. The arrangement and number of the wing base sclerites in Neoptera is also assumed as an apomorphy of Neoptera (MATSUDA 1970). On the other hand KUKALOVÁ-PECK (1983, 1987, 1991) assumed that the few wing base sclerites in Ephemeroptera and Odonata are the result of a secondary fusion. According to KUKALOVÁ-PECK (1983,

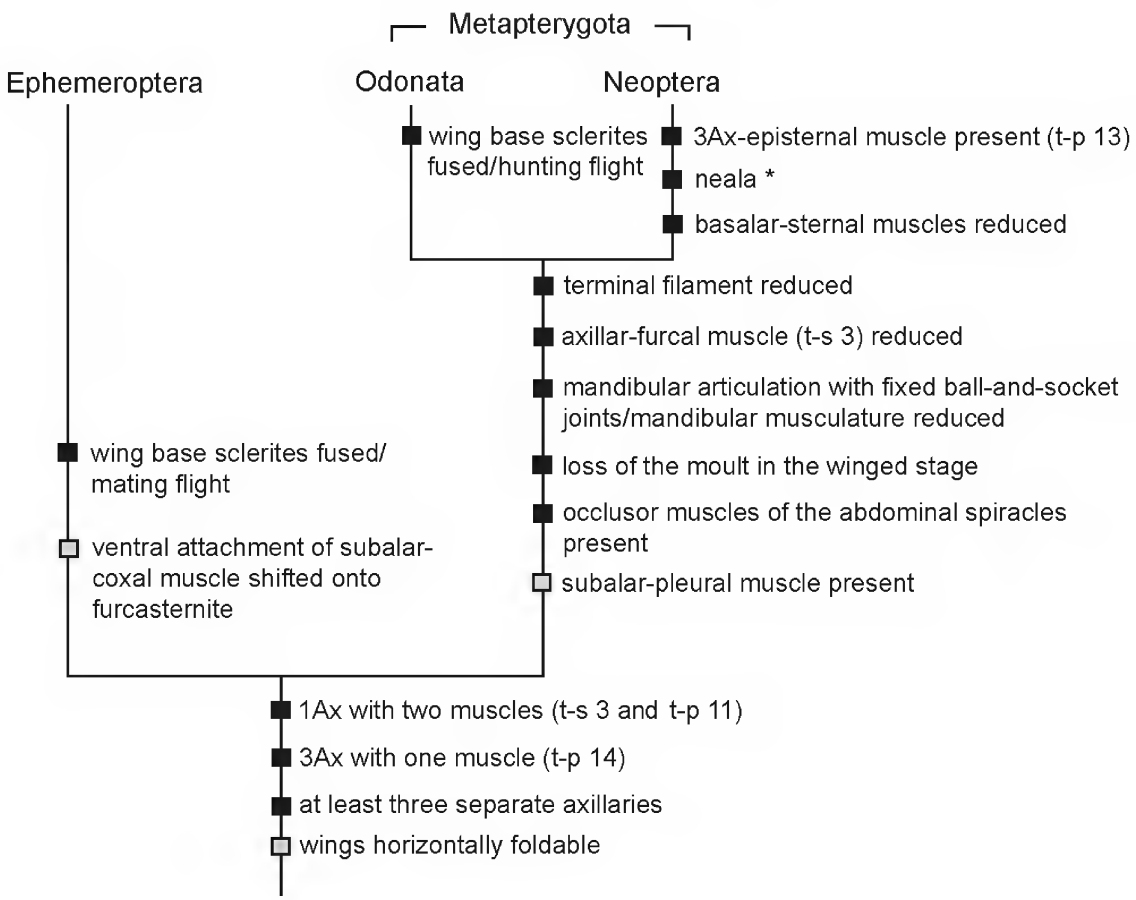

Fig. 127. Metapterygota hypothesis, argumentation scheme of character evolution (modified after Willkommen & Hörnschemeyer 2007: fig. 25). – * = character after Martynov (1925); for further interpretation see section 4.4.

1987, 1991), the wing base consists of 32 sclerites in the pterygote ground plan. As a consequence she considered the condition in the Ephemeroptera and Odonata as apomorphic. With reference to Kukalová-Peck (1974b), Boudreaux (1979) also suggested that the sclerites of the wing base in Ephemeroptera are probably a result of a secondary fusion correlated with their weak flight ability. Yet the paleopterous wing resting position was assumed as a primitive character of mayflies by Boudreaux (1979).

The fossil Diaphanopterodea are generally classified within the otherwise paleopterous Palaeodictyopterida, although they are characterised by the ability to fold the wings horizontally over the abdomen (Kukalová-Peck 1974a, 1974b). Given the fact that all three basal extant pterygote lineages exhibit the t-p 14 (the wing flexor muscle, which is said to be responsible for the horizontal wing flexion in Neoptera), it seems to be straightforward to assume that the horizontal wing folding is a ground plan character of Pterygota. Nevertheless, due to the different wing base elements of Diaphanopterodea and Neoptera most authors assumed that the ability to fold the wings horizontally over the abdomen evolved convergently (Kukalová-Peck 1974a, 1974b, 1978, 1983; Wootton 1979; Wootton & Kukalová-Peck 2000). In contrast, Brodsky (1994), Kukalová-Peck (1991), Rasnitsyn (2002) and Willmann (1998) assumed a loss of the ability to fold the wings horizontally over the abdomen in Odonata and Ephemeroptera (see section 4.4). This assumption suggests wing folding as a ground plan character of Pterygota. The Lepidoptera, however, are an indication that this scenario could be quite possible. Within this taxon, the Papilionoidea lost the ability to fold the wings horizontally over the abdomen. The Papilionoidea are also characterised by a flight behaviour that includes short phases of gliding flights with locked wing positions. Yet the wing base elements are not fused in the Papilionoidea (Ivanov 1995, 1996, 1997; Sharplin 1963a, b).

Following Kukalová-Peck (1983, 1987, 1991), Brodsky (1994) hypothesised a fusion of the wing base sclerites in Ephemeroptera and Odonata, but originating from a condition that was more similar to the neopteran wing base with only few wing base sclerites.

A synapomorphic fusion of the wing base sclerites in Ephemeroptera and Odonata cannot be excluded but is rather unlikely. Both Ephemeroptera and Odonata have a flight system that is specialised in different ways: Ephemeroptera have a reduced metathorax with small or even absent hind wings. Both hind and fore wings are coupled in flight. Furthermore, Ephemeroptera are characterised by a specialised mating flight that is usually performed along a more or less vertical axis. Odonata are adapted to a manoeuvrable hunting flight. Meso- and metathorax of Odonata are fused to an obliquely orientated synthorax. Together with the legs it forms the characteristic capture apparatus.

Thus all the characters mentioned above are autapomorphic for the Ephemeroptera and Odonata, respectively. The different adaptations to dissimilar flight behaviour are reflected by the fusion of 2Ax with PMP in the Ephemeroptera on the one hand and the fusion of at least 2Ax and 3Ax with PMP in Odonata on the other hand. This may suggest that the strengthening of the wing base in both taxa evolved independently in both lineages.

Metapterygota hypothesis

The Metapterygota hypothesis assumes a sister group relationship between Ephemeroptera and Metapterygota (Odonata+Neoptera). It is supported by the following apomorphic characters of the Metapterygota: Mandibular articulation with fixed ball-and-socket joints, reduction of the Musculus mandibulo-hypopharyngealis, reduction of several mandibular abductor and adductor muscles, and the presence of occlusor muscles of the abdominal spiracles (Börner 1909; Fürst von Lieven 2000; Hennig 1953; Kristensen 1975, 1981, 1991; Staniczek 2000, 2001). Furthermore, Odonata and Neoptera lack the ecdysis in a winged stage and the terminal filament is reduced (Edmunds & McCafferty 1988, Kristensen 1981, Staniczek 2001). According to Willmann (2005) a modified terminal filament is present in the fossil odonatan taxon *Namurotypus*. Consequently this character should not be upheld as synapomorphy of the Metapterygota.

According to Matsuda (1970) an axillar-furcal muscle is only present in Ephemeroptera but lost in Metapterygota, suggesting a closer relationship of Odonata+Neoptera.

The development of a subalar-pleural muscle is also regarded as a potential apomorphy of Metapterygota, because this muscle is present in Odonata and Plecoptera.

The pleural arm and its associated muscle p-s 1 sensu Matsuda (1970), which is attached to the furca ventrally are probably ground plan characters of Dicondylia. Both characters are absent in Ephemeroptera and adult Odonata. The presence of this muscle in larval Odonata, however, may indicate that the reduction of the pleural arm and the associated muscle in adult Ephemeroptera and Odonata evolved independently.

The subalar-sternal muscle (SA.Sm) is generally assumed to be only present in mayflies (Brodsky 1994). The dorsal attachment and ontogenetical development of the subalar-sternal muscle in larval Ephemeroptera is, however, identical to that of the subalar-coxal muscle of larval Plecoptera (see section 4.3.7). So I assume these muscles to be homologous. It is, however, not clear whether the ventral attachment at the furcasternum (in Ephemeroptera) or at the posterior coxal rim (in Odonata and Neoptera) represents the groundplan condition of Pterygota. According to Brodsky (1974) the sternal attachment of this muscle represents a specialisation of the wing apparatus of Ephemeroptera. Indeed, the enlargement of the SA.Sm that obviously took place in Ephemeroptera might be correlated with an enlargement of its points of attachments. As a consequence, the subalare of Ephemeroptera got enlarged and the SA.Sm shifted ventrally to the furcasternum. In any case a putative loss of the subalar-sternal muscle as autapomorphy of Metapterygota cannot be uphold anymore, as a homologue of this muscle is present in both Odonata and Neoptera.

Ephemeroptera and Odonata have two anterior "basalar muscles" that are attached to the crescent-shaped sclerite in Ephemeroptera (BA.SmS/BA.SmI) and to the anterior part of the humeral plate in Odonata (muscles 21 and 22). These two muscles are without much doubt homologous in Ephemeroptera and Odonata. Homologous muscles are most likely not present in Neoptera but in Zygentoma. Therefore, the presence of these muscles is a symplesiomorphic character of Ephemeroptera and Odonata. The absence of these muscles is an apomorphic character of Neoptera. Thus, neither presence nor absence of the so-called basalar-sternal muscles is citable as a character supporting the Palaeoptera or the Metapterygota hypothesis.

Previous authors (e. g. Hennig 1969, Gullan & Cranston 2005) assumed that the low amount of wing base sclerites represents a primitive condition: Ephemeroptera have a free 1Ax and a partly free 3Ax, whereas in Odonata only one free wing base sclerite is present. However, as shown above, Ephemeroptera and Odonata are in all probability apomorphic concerning the wing base sclerites, i. e. the sclerites are partially fused. This does not necessarily imply a synapomorphic fusion in Ephemeroptera and Odonata. Morphological characters (absence of the subimago, mandible characters including autapomorphic characters of Metapterygota; compare Staniczek 2001) rather support a sister group relationship of Odonata+Neoptera (Metapterygota). Based on the current knowledge it is rather unlikely to assume a homologous fusion of the wing base sclerites. Moreover, the Ephemeroptera and Odonata are adapted to different types of flight by reason of different flight behaviour. Brodsky (1994) mentioned that the development of gliding flight was accompanied by the development of platforms in the

wing bases. He assumed an independent occurrence in Ephemeroptera and Odonata. Surely, it is not impossible to hypothesise a homologous fusion of the wing base sclerites in Ephemeroptera and Odonata, though it is rather unlikely (see above).

4.5 Evolution of the wing folding mechanism

Both Ephemeroptera and Odonata are adapted to special kinds of flight. Odonata are adroit and extremely manoeuvrable flying hunters. They have a remarkably adapted morphology of the pterothoracic sclerites and flight musculature.

The flight system of Ephemeroptera is characterised by a specialised mesothorax with a large dorsal longitudinal muscle and a small metathorax with short hind wings. Shortly after their emergence the Ephemeroptera begin their impressive nuptial dances. Associated with the swarming behaviour the Ephemeroptera are adapted to a special gliding flight and parachuting and especially males are adapted to a persistent vertical mating flight Brodsky (1973, 1994). Brodsky (1973) distinguished between four types of swarming. In the first type of swarming the emergence of the subimago may be more or less prolonged in time (e. g. Baetidae, Ephemerellidae, Ephemeridae, Leptophlebiidae, Siphlonuridae). Oligoneuriidae, Palingeniidae and Polymitarcyidae have a swarming behaviour where the nuptial dances take place in form of a rapid horizontal flight usually close to the surface of the water. Fischer (1991) differentiated between eight types of swarming dependent on the trajectory of the mayflies. The ability to lock the wings in the gliding position correlates with the presence of SA.Fm, Ax.Fm and Ax.PmI or rather at least one of those muscles (Brodsky 1974). Usually, only males are known to perform the vertical nuptial dances. Fischer also noticed a vertical flight in some female specimens. Therefore, the ability to lock the wings in the gliding position as well as the presence of SA.Fm, Ax.Fm and Ax.PmI is expected to exist also in female specimens.

According to Fischer (1991), the problems resulting from the inability to fold the wings horizontally over the abdomen (such as no longer being able to hide from hunters in crevices, being caught in cobwebs etc.) are negligible when living dependent on a substrate. Mayflies spend indeed a lot of their adult life span in the air. The inability to fold the wing does not have to be necessarily only a disadvantage. Furthermore, the steep upward flights and the perpendicular gliding flights are – according to Fischer – only attainable with a morphological specialisation. The loss of the wing folding for example would be conceivable as such a specialisation.

The dorsal longitudinal muscles of the mesothorax of Ephemeroptera are enlarged and require at least one-half of the height of the mesothorax. The metathorax, in contrast, is short, bearing short hind wings not exceeding one half of the fore wing length. The hind wings are often coupled with the fore wings in flight. Compared to other pterygote insects this is an apomorphic condition. Also the Odonata show apomorphic conditions in their flight system, e. g. the fusion of both meso- and metathorax to the characteristic synthorax, correlated with the hunting flight.

Regarding the specialisations of the ephemeropteran and odonatan flight systems, concerning their flight behaviour, it can be hypothesised that the wing base is secondarily stiffened in both taxa. The wing base elements of Ephemeroptera are at least partly a result of a secondary fusion (2Ax+PMP, see above), the 3Ax is closely associated with BP (2Ax+PMP) and both the anal and costal brace support more stability at the wing base during gliding flight. This assumption is also supported by the fact that the wing veins in fossil mayflies, the Protereismatidae, are distinct even to the point of the wing base (Kukalová-Peck 1974b). Large and apparently functional mouthparts were still present in Permian mayflies. Based on this knowledge Kukalová-Peck (1974b: 420f) believed that the horizontal flight was more important in these taxa than in extant Ephemeroptera. Furthermore, she supposed that the obliteration of the adjacent stems probably occurred later in evolution.

In the present work it is assumed that the wing base in the ground plan of Pterygota consists of four separate sclerites that are arranged approximately as in the extant Plecoptera.

If one assumes that the Palaeoptera is monophyletic and the inability to fold the wings horizontally over the abdomen is a plesiomorphic character, the question remains if the secondary fusion of the wing base sclerites in Ephemeroptera and Odonata evolved convergently or as a synapomorphy of both taxa.

Currently, there are more characters supporting the Metapterygota hypothesis. Based on this assumption the evolutionary pathway of wing base development in Pterygota is assumed as follows: The wing base in the groundplan of Pterygota is composed of four wing base sclerites (1Ax, 2Ax, 3Ax, PMP). Convergently, the wing base is strengthened and different elements are partially fused in Ephemeroptera and Odonata. In Ephemeroptera the wing base is stiffened (2Ax+PMP) as an adaptation for the vertical mating flight and for the parachuting phases in flight. In contrast the wing base elements of Odonata may be fused (at least 2Ax+PMP+3Ax) as an adaptation to their highly manoeuvrable hunting flight.

In consideration of the special kinds of flight in Ephemeroptera and Odonata together with the presence of an axillar-pleural muscle (t-p 14) in both orders, which is homologous with one of the wing flexor muscles in Neoptera, it is a legitimate question whether the inability

to fold the wings horizontally over the abdomen is a plesiomorphic or an apomorphic character. If one assumes a wing base configuration almost similar to that of the Plecoptera in the ground plan of Pterygota, horizontal wing folding may also have been possible.

Already Brodsky (1970: 188) summarised that all the elements needed for horizontal wing folding are present on the mesothorax of *E. vulgata*: a third axillary sclerite, a pleuroalar muscle and an anal-jugal wing fold. However, the function of these formations differs from their function in insects of other orders, which fold their wings over the abdomen. According to Brodsky (1994: 91), Ephemeroptera and Odonata have lost the ability to fold their wings; consequently, the muscle t-p 14 has changed its function.

The fossil Diaphanopterodea combine apomorphic characters of the Palaeodictyopterida (haustellate mouthparts) with the ability to fold the wings horizontally over the abdomen (Kukalová-Peck 1974a). Therefore, this author assumed that wing folding arose at least twice in insects (Kukalová-Peck 1974a, 1974b; Kukalová-Peck & Brauckmann 1990). Wootton (1979, 1981) and Wootton & Kukalová-Peck (2000) come to the same conclusion. Unlike these assumptions Willmann (1998: 274) suggested that the ability to fold the wings horizontally over the abdomen could be a plesiomorphic condition and that there is no need to view wing folding in the Neoptera and Diaphanopterodea as a result of convergence. This scenario could be indeed quite possible.

A loss of the ability to fold the wings in Ephemeroptera is also assumed by Brodsky (1994) and Rasnitsyn (2002). The latter wrote that a loss of the wing flexing is supported by the fact that Ephemeroptera retain a suture that separates the posterior articulatory process of the basal plate (equivalent to s3 or 3Ax of the present study) and the rest of the basal plate, which precludes flexibility. Following this author, the posterior articulatory process, however, is clearly the 3Ax and the mentioned suture is actually not a suture but the border between the two, mostly separate, sclerites, i. e. the BP and the 3Ax. Nevertheless, the morphology of the ephemeropteran wing base enables indeed no flexibility.

If one assumes that wing folding is a plesiomorphic character and that the Metapterygota are monophyletic, the ability to fold the wings was lost at least three times during the early evolution of the Pterygota. A convergent loss of the ability to fold the wings horizontally is in any case also present in the holometabolous Papilionidae (Neoptera: Lepidoptera) (Ivanov 1996).

The hypothesis that wing folding is a plesiomorphic character of Pterygota is not supported by paleontological evidence. The fossil Palaeodictyopterida (sensu Grimaldi & Engel 2005) is often treated as a monophyletic group that is characterised by its haustellate mouthparts (Kukalová-Peck 1991). This taxon presumably contains the paraphyletic Palaeodictyoptera (Grimaldi & Engel 2005, Bechly pers. comm.), the Megasecoptera, the Diaphanopterodea and the Permothemistida. That means that the ability to move the wings to a resting position over the abdomen must have been reduced several times within the paraphyletic Palaeodictyoptera, in the Ephemeroptera, and in the Odonata. Nevertheless, according to Willmann (2003) the Palaeodictyopterida may be a paraphyletic assemblage, as the presence of haustellate mouthparts is not confirmed in all taxa of Palaeodictyopterida. As a consequence it remains difficult to include these fossil taxa into the present argumentation until better information on their character distribution is available and the relationships among fossil taxa become better resolved.

5 Conclusions and future prospects

The wing base in the ground plan of Pterygota is most likely composed of four wing base sclerites. Three of these four sclerites are the first axillary (1Ax), the second axillary (2Ax) and the third axillary (3Ax). In all probability the proximal median plate (PMP) is also a ground plan character of Pterygota. The 1Ax and the 3Ax are equipped with muscles. At least one muscle running to the pleurum inserts at the 1Ax. This muscle is present in Ephemeroptera and in Plecoptera. Most likely, a second muscle running from the 1Ax to the furca is present in the pterygote ground plan. This muscle is retained only in Ephemeroptera. Furthermore, a muscle running from the upper part of the pleurum to the 3Ax is present in the pterygote ground plan (t-p 14 sensu Matsuda 1970). This muscle is one of the wing flexor muscles of Neoptera but it is also present in the wing bases of Ephemeroptera and Odonata. In Plecoptera two muscles are attached to the 3Ax (t-p 13 and t-p 14). Muscle t-p 13 sensu Matsuda (1970) is most likely a ground plan character of Neoptera.

The wing base of Ephemeroptera is composed of sclerites that can be homologised with the axillaries of Neoptera. The 1Ax is provided with two muscles in primordial Ephemeroptera. The 2Ax is fused to the basal plate (BP) in Ephemeroptera. The BP of Ephemeroptera is most likely a product of a fusion of the base of the anterior radial vein, the proximal median plate and the 2Ax. The 3Ax of Ephemeroptera is tightly connected to the basal plate but not completely fused to it, even in basal Ephemeroptera.

The anterior humeral plate of the wing base of Odonata is probably composed of the humeral plate (HP) and of a sclerite that is homologous to the so-called basalar sclerite of Ephemeroptera. Two muscles are attached to the lateral area of the humeral plate by a tendon. These two muscles are probably homologous to the BA.SmS and BA.SmI of Ephemeroptera. The axillary plate of the Odo-

nata is in all probability a result of a fusion of the 2Ax, the PMP and the 3Ax. The posterior area of the axillary plate (3Ax) serves as the insertion point of a short muscle that is homologous to the t-p 14 sensu MATSUDA (1970). The small sclerite that lies proximal to the humeral plate is rather a part of the prescutum than the 1Ax, as has been previously suggested (TANNERT 1958). A muscle running from the 1Ax to the pleurum was absent in the examined Odonata. Moreover, a sclerite homologous to the 1Ax of Neoptera is not obvious in the wing base of Odonata.

The basalar muscles (BA.SmS, BA.SmI and BA.Cm) of Ephemeroptera are of tergal origin. The so-called basalar-pleural muscle (BA.Pm) of Ephemeroptera is not a true basalar muscle. It is homologous with a short muscle that is attached to a tergal sclerite in Odonata (muscle 28) and to t-p 4, which is attached to the subtegula in Neoptera. A basalar-trochanteral muscle (BA.Trm), which was described in previous contributions, was not found in any of the examined Ephemeroptera.

The subalar-sternal muscle (SA.Sm) of Ephemeroptera is characterised by the same ontogenetically development in larvae as the subalar-coxal muscle of Neoptera (t-cx 8), whereas the subalar-coxal muscle (SA.Cm) of Ephemeroptera shows a different origin to t-cx 8 of Neoptera. This suggests that the subalar-coxal muscle of Ephemeroptera is not homologous to t-cx 8 of Neoptera. The SA.Sm of Ephemeroptera, however, is clearly homologous to t-cx 8 of Neoptera, rather than being a primitive muscle, which is only present in Ephemeroptera and absent in Neoptera.

The wing base structure and also the morphology of the pterothorax and the specialised flight musculature of Ephemeroptera and Odonata, together with their flight behaviour, suggest that these taxa are more advanced than previously assumed. Furthermore, the inability to fold the wings horizontally over the abdomen could be a result of a secondary strengthening and partially fusion of the wing base sclerites. The Plecoptera, usually regarded as sistergroup to the remaining Neoptera or of the remaining Polyneoptera, are most likely very close to the ground plan of the Pterygota in many respects.

The innervation of the muscles associated with the basalar-complex of Ephemeroptera, Odonata and Neoptera should be further examined to verify their homology. The musculature and the innervation of the muscles in Zygentoma should be examined with particular attention paid to the muscles that are homologised with those of Pterygota. Additionally, the fate of prospective thoracic muscles in the larvae of basal pterygotes may possibly be investigated to gain more clues on their homologies in the future.

The comparison of the basalar and subalar complex of Lepidoptera and Ephemeroptera could be rewarding from a point of comparative functional morphology.

Besides a more detailed morphological comparison of Zygentoma and Pterygota, the unravelling of the relationships among the Palaeodictyopterida would be of great value to gain new arguments for a decision between the Palaeoptera or Metapterygota hypothesis.

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Manuscript received: 3.IX.2007, accepted: 9.XI.2007.

A revision of the *Micrillus* species of the Palaearctic region, with notes on two species from adjacent parts of the Afrotropical and Oriental regions (Coleoptera: Staphylinidae: Paederinae)

Volker Assing

Abstract

The species of the paederine genus *Micrillus* Raffray, 1873 of the Palaearctic region, as well as of the adjacent parts of the Afrotropical and Oriental regions are revised. In the Palaearctic region, the number of valid names is significantly reduced, from 24 to 10. Twelve species, two of them from the Afrotropical and the Oriental regions, respectively, are (re-)described, and illustrated. They are attributed to two species groups, the *M. testaceus* group including eight species from the Western Palaearctic region (including Middle Asia) and the *M. aegyptiacus* group with four species from the south of the Western Palaearctic, the north of the Afrotropical, and the Oriental regions. Two new species are described: *M. tenuipennis* **n. sp.** (Morocco) and *M. sudanicus* **n. sp.** (Sudan). The following synonymies are proposed: *Micrillus testaceus* (Erichson, 1840) = *Scymbalium grandiceps* Jacquelin du Val, 1853, **resyn.**, = *S. pubipenne* Fairmaire, 1860, **n. syn.**, = *S. longipenne* Brisout de Barneville, 1863, **n. syn.** (previously a synonym of *S. pubipenne*), = *Schatzmayria tergestina* Gridelli, 1914, **n. syn.** (previously a synonym of *S. pubipenne*), = *Scymbalium zuercheri* Wanka, 1914, **n. syn.**, = *Micrillus libanicus* Coiffait, 1980, **n. syn.**, = *M. hispanicus* Coiffait, 1980, **n. syn.**, = *M. zacinthicus* Coiffait, 1980, **n. syn.**, = *M. syriacus* Coiffait, 1980, **n. syn.**, = *M. calabricus* Coiffait, 1980, **n. syn.**, = *M. turcicus* Coiffait, 1980, **n. syn.**, = *M. graecus* Coiffait, 1980, **n. syn.**, = *M. cypriacus* Coiffait, 1980, **n. syn.**, = *M. corcyranus* Coiffait, 1980, **n. syn.**, = *M. brekhovi* Grebennikov, 2001, **n. syn.**; *Micrillus pallidus* Reitter, 1887 = *M. caucasicus* Coiffait, 1980, **n. syn.**; *Micrillus aegyptiacus* (Bernhauer, 1910) = *Scymbalium bernhaueri* Koch, 1934, **n. syn.**; *M. torretassoi* (Koch, 1934) = *Scymbalium collare* Scheerpeltz, 1962, **n. syn.**; *Pseudomedon dido* (Saulcy, 1865) = *Scymbalium minimum* Eppelsheim, 1888, **n. syn.** Several previously established synonymies are confirmed. The binomen *Micrillus indicus* (Eppelsheim, 1890), **n. comb.** (ex *Scymbalium*) is established. Lectotypes are designated for *Scymbalium testaceum* Erichson, *S. biskrense* Fauvel, *S. scabrosum* Fauvel, 1875, *S. hypogaeum* Peyerimhoff, 1907, *S. bernhaueri* Koch, *S. torretassoi* Koch, and *Medon apfelbecki* Bernhauer, 1899. The distributions of 12 species are mapped. A key to species and a synonymic catalogue of *Micrillus* are provided.

Keywords: Staphylinidae, Paederinae, *Micrillus*, *Scymbalium*, *Pseudomedon*, Palaearctic region, Afrotropical region, Oriental region, taxonomy, morphometry, new species, new synonymies, lectotype designations, dimorphism, bionomics, distribution, seasonal distribution, catalogue, key to species.

Zusammenfassung

Die paläarktischen Arten der Gattung *Micrillus* Raffray, 1873 werden revidiert. Die Zahl der in der Paläarktis vertretenen validen Arten verringert sich von 24 auf 10. Zwölf Arten, davon zwei aus der Afrotropis bzw. der Orientalis werden beschrieben und abgebildet. Zwei Artengruppen werden unterschieden: die *M. testaceus*-Gruppe mit acht in der Westpaläarktis (einschließlich Mittelasien) verbreiteten Arten und die *M. aegyptiacus*-Gruppe mit vier Arten in der südlichen Westpaläarktis, der nördlichen Afrotropis und der Orientalis. Zwei Arten werden erstmals beschrieben: *M. tenuipennis* **n. sp.** (Marokko) und *M. sudanicus* **n. sp.** (Sudan). Die Revision ergab die folgenden Synonymien und Neukombination: *Micrillus testaceus* (Erichson, 1840) = *Scymbalium grandiceps* Jacquelin du Val, 1853, **resyn.**, = *S. pubipenne* Fairmaire, 1860, **n. syn.**, = *S. longipenne* Brisout de Barneville, 1863, **n. syn.** (bisher Synonym von *S. pubipenne*), = *Schatzmayria tergestina* Gridelli, 1914, **n. syn.** (bisher Synonym von *S. pubipenne*), = *Scymbalium zuercheri* Wanka, 1914, **n. syn.**, = *Micrillus libanicus* Coiffait, 1980, **n. syn.**, = *M. hispanicus* Coiffait, 1980, **n. syn.**, = *M. zacinthicus* Coiffait, 1980, **n. syn.**, = *M. syriacus* Coiffait, 1980, **n. syn.**, = *M. calabricus* Coiffait, 1980, **n. syn.**, = *M. turcicus* Coiffait, 1980, **n. syn.**, = *M. graecus* Coiffait, 1980, **n. syn.**, = *M. cypriacus* Coiffait, 1980, **n. syn.**, = *M. corcyranus* Coiffait, 1980, **n. syn.**, = *M. brekhovi* Grebennikov, 2001, **n. syn.**; *Micrillus pallidus* Reitter, 1887 = *M. caucasicus* Coiffait, 1980, **n. syn.**; *Micrillus aegyptiacus* (Bernhauer, 1910) = *Scymbalium bernhaueri* Koch, 1934, **n. syn.**; *M. torretassoi* (Koch, 1934) = *Scymbalium collare* Scheerpeltz, 1962, **n. syn.**; *Pseudomedon dido* (Saulcy, 1865) = *Scymbalium minimum* Eppelsheim, 1888, **n. syn.**, *Micrillus indicus* (Eppelsheim, 1890), **n. comb.** (ex *Scymbalium*). Für *Scymbalium testaceum* Erichson, *S. biskrense* Fauvel, *S. scabrosum* Fauvel, 1875, *S. hypogaeum* Peyerimhoff, 1907, *S. bernhaueri* Koch, *S. torretassoi* Koch und *Medon apfelbecki* Bernhauer, 1899 werden Lectotypen designiert. Die derzeit bekannte Verbreitung der untersuchten *Micrillus*-Arten wird anhand von Karten illustriert. Ein Katalog der Arten einschließlich aller Synonyme und eine Bestimmungstabelle werden erstellt.

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1 Introduction and taxonomic history

The genus *Micrillus* was described by Raffray (1873), who distinguished it from *Achenium* Leach, 1819 based on the morphology of the metatarsi and the strongly reduced eyes, but did not explicitly refer to *Scymbalium* Erichson, 1839, which at that time comprised all the described species later to be attributed to *Micrillus*. The only species originally included was the microphthalmous type species (by monotypy) *M. subterraneus* Raffray, 1873 from Algeria. *Micrillus* was subsequently synonymised with *Scymbalium* by Fauvel (1875), who continued to treat the name as a synonym also in later papers (e. g. Fauvel 1886, 1898, 1902). His view was widely accepted in the decades to come, e. g. by Peyerimhoff (1907), who described another microphthalmous species from Algeria, *Scymbalium hypogaeum*, and keyed the six *Scymbalium* species known from North Africa at that time, as well as in the catalogue by Bernhauer & Schubert (1912).

In a key to the Palaearctic species of *Scymbalium*, which included nine names today attributed to *Micrillus*, Wanka (1914) described a new species, *S. zuercheri* from Turkey.

Gridelli (1914) described the genus *Schatzmayria*, suggesting close affiliations to *Scymbalium* and *Euphonus* Fauvel, 1902 (today a subgenus of *Pseudomedon* Mulsant & Rey, 1878) and separating it from these taxa by the simple (undilated) protarsi in both sexes and by the shape of the palpi. He included two new species in the genus, *S. meridionalis* – which was later designated as the type species by Blackwelder (1939) – and *S. tergestina*, without reference to closely related species, which were still attributed to *Scymbalium*. Made aware of the presence of other species with simple protarsi by A. Dodero, an Italian contemporary, he regarded *Schatzmayria* as a subgenus of *Scymbalium* a few years later, synonymised *Schatzmayria meridionalis* with *Scymbalium testaceum* Erichson, 1840 and *Schatzmayria tergestina* with *Scymbalium pubipenne* Fairmaire, 1860; also, he included three additional species, *Scymbalium (Schatzmayria) pallidum* Reitter, 1887, *S. (S.) hypogaeum*, and *S. (S.) subterraneum*, disregarding the priority of the senior name *Micrillus* (Gridelli 1921). This priority later also escaped the attention of Scheerpeltz (1933) and Blackwelder (1952).

In a synopsis of the *Scymbalium* species of India, Burma, and Ceylon, Cameron (1931) listed four species, one of them, *S. indicum* Eppelsheim, 1890, now attributed to *Micrillus*.

Scheerpeltz (1962) considered the separation of the subgenera *Scymbalium* and *Schatzmayria* unjustified, emphasised the isolated position of *Scymbalium anale* (Nordmann, 1837), and presented an updated key to 14 Palaearctic species of *Scymbalium*, one of them new (*S. collare* from Sudan). Remarkably, he – correctly – omitted *S. minimum*, but without comment.

Coiffait (1980, 1982) eventually recognised the synonymy of *Schatzmayria* with *Micrillus* and separated the latter from *Scymbalium* as a distinct genus, based on the simple undilated protarsi, the more slender and glabrous fourth joint of the maxillary palpus, the position of the aedeagus in the abdomen, as well as the almost completely reduced parameres of the aedeagus. In the same paper, he

described ten new species and a new variety (unavailable name) from the Mediterranean, and presented a key to the 24 species he considered valid. Since then, only one species has been added to the genus, *M. brekhovi* from Russia, by GREBENNIKOV (2001), so that the genus included 25 valid nominal taxa, 24 of them from the Palaearctic region (SMETANA 2004) and one from the Afrotropical region.

The present revision was stimulated especially by the repeated difficulties encountered when trying to clarify the specific identities of *Micrillus* from the Mediterranean. The identification results obtained using the keys by COIFFAIT (1980, 1982) were usually highly doubtful and rarely corresponded with the biogeographic data indicated in the literature, observations shared also by other colleagues. This, as well as the fact that, according to the illustrations provided by COIFFAIT (1980, 1982), the aedeagi of several species were practically indistinguishable, and, finally, new evidence suggesting that at least some of the "taxa" were wing-dimorphic and subject to pronounced intraspecific variation raised the suspicion that the taxonomic confusion in the genus was possibly the result of a high degree of synonymy.

Acknowledgements

My thanks are extended to all the colleagues indicated in the material section for the loan of material under their care. MARC TRONQUET, Molitg-les-Bains, and ANDREAS PÜTZ, Eisenhüttenstadt, assisted with the identification of some localities. LEE HERMAN, New York, kindly communicated an excerpt from an unpublished world catalogue of Paederinae, with the names of all the species currently in *Scymbalium*, and including relevant literature references. The critical comments of the two reviewers, BENEDIKT FELDMANN, Münster, and MICHAEL SCHÜLKE, Berlin, are appreciated.

2 Material, methods, and depositories

Altogether 910 specimens of *Micrillus* were examined, among them the available types. The material is deposited in the following public institutions and private collections:

BMNH The Natural History Museum, London (R. BOOTH)
cAnl private collection S. ANLAŞ, Turgutlu
cAss author's private collection
cFel private collection B. FELDMANN, Münster
cGon private collection A. GONTARENKO, Odessa
cSch private collection M. SCHÜLKE, Berlin
cTro private collection M. TRONQUET, Molitg-les-Bains
cWun private collection P. WUNDERLE, Mönchengladbach
cZan private collection A. ZANETTI, Verona
DEI Deutsches Entomologisches Institut, Müncheberg (L. ZERCHE)
FMNH Field Museum of Natural History, Chicago (J. BOONE, A. NEWTON)
HNHM Hungarian Natural History Museum, Budapest (GY. MAKRANCZY, O. MERKL)
IRSNB Institut royal des Sciences naturelles de Belgique (Y. GÉRARD)
MCSNM Museo Civico di Storia Naturale di Milano (F. RIGATO)
MHNG Muséum d'Histoire naturelle, Genève (G. CUCCODORO)
MNCN Museo Nacional de Ciencias Naturales, Madrid (I. IZQUIERDO)
MNHNP Muséum National d'Histoire naturelle, Paris (A. TAGHAVIAN)
MNHUB Museum für Naturkunde der Humboldt-Universität zu Berlin (J. FRISCH, M. UHLIG, J. WILLERS)
NHMW Naturhistorisches Museum Wien (H. SCHILLHAMMER)
SMF Senckenberg-Museum Frankfurt/Main (A. HASTENPFLUG-VESMANIS)
SMNS Staatliches Museum für Naturkunde, Stuttgart (W. SCHAWALLER, K. WOLF-SCHWENNINGER)
SMTD Staatliches Museum für Tierkunde, Dresden (O. JÄGER)
TAU National Museum of Natural History, Tel Aviv University (A. FREIDBERG, via B. FELDMANN)
ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg (B. KATAEV, via V. GUSAROV)

The morphological studies were conducted using a Stemi SV 11 microscope (Zeiss Germany) and a Jenalab compound microscope (Carl Zeiss Jena) with a drawing tube. For the photographs a digital camera (Nikon Coolpix 995) was used. The maps were generated using the online generic mapping tool (GMT) of the Geomar website at www.aquarius.ifm-geomar.de/omc.

In order to assess intraspecific variation, 468 specimens were measured. The following morphological parameters were examined:

AL length of antenna
EL length of elytra along suture, from apex of scutellum to posterior margin
EyL length of eye in lateral view
HL head length from anterior margin of frons to neck
HW maximal head width
ML length of aedeagus from base to apex of ventral process
PL length of pronotum along midline
POL length of postocular region from posterior margin of eye to posterior margin of head (lateral view)
PW maximal width of pronotum
TaL length of metatarsus
TiL length of metatibia
TL body length from mandibles to posterior margin of abdominal tergite VIII

Maximum/minimum ratios are used to estimate the extent of intraspecific variation of size-related parameters and are given as the maximal value divided by the minimal value of a particular parameter. In the diagrams, size is given as the sum of the approximated surface areas of head and pronotum (HL×HW+PL×PW).

The concept of the zoogeographic regions used here is in accordance with that proposed by LÖBL & SMETANA (2004).

Labels of type material are cited in their original spelling and language, except for the following adaptations according to the general format requirements of the journal: names of persons (except authors of species) in small capitals, scientific names of genera and species in italics, dates with the months always in Roman numbers.

3 Results

3.1 The genus *Micrillus* Raffray

3.1.1 Diversity, zoogeography, and systematics

The revision of the available types and non-type material from practically all the major collections revealed a taxonomic confusion of truly remarkable dimensions. In all, 17 new synonymies in *Micrillus* and one in *Pseudomedon* are proposed, one previously revalidated name is resynonymised, and only two new taxa are described. The number of valid names in *Micrillus* is reduced by 60%, from 25 to 10, disregarding two species – one of them new and one of them transferred from *Scymbalium* – whose distribution is clearly outside the Palaearctic region. *Micrillus testaceus* alone has as many as 19 junior synonyms.

The reasons for such a high degree of synonymy are manyfold. Even in the larger collections, material of *Micrillus* species is comparatively scarce, and the descriptions of almost all the names are based on only one or few specimens from usually one locality. Coiffait (1982) alone described 10 species; all of these names are now synonyms, nine of *M. testaceus* and one of *M. pallidus*. Although he described more *Micrillus* species than anyone else, his collection at the MNHNP contains only 44 specimens, most of them types (Fig. 1). With so little material available for comparison, an adequate assessment of intraspecific variation – especially of widespread species – is impossible. Some species of *Micrillus*, *M. testaceus* in particular, are subject to pronounced intraspecific variation especially of various size-related parameters, head shape and relative head size, and coloration. Two species are wing-dimorphic, this dimorphism not only involving the length of the hind wings, but also the length of the elytra, eye size, occasionally the shape of the head, as well as the coloration. Finally, as is often the case especially with wing-dimorphic species, the distribution ranges have been underestimated. This is particularly true of *M. testaceus*, whose macropterous morph is rarer than the brachypterous morph and has been collected on the wing, which proves that parts of the populations are capable of flight and long-distance dispersal. Another example is provided by *M. torretassoi*, whose brachypterous morph was described from northern Egypt by Koch (1934) and whose macropterous morph was later described as a distinct species, *Scymbalium collare*, from southern Sudan

Fig. 1. Drawer from the Coiffait collection at the MNHNP containing his material of *Micrillus* (highlighted by black frame).

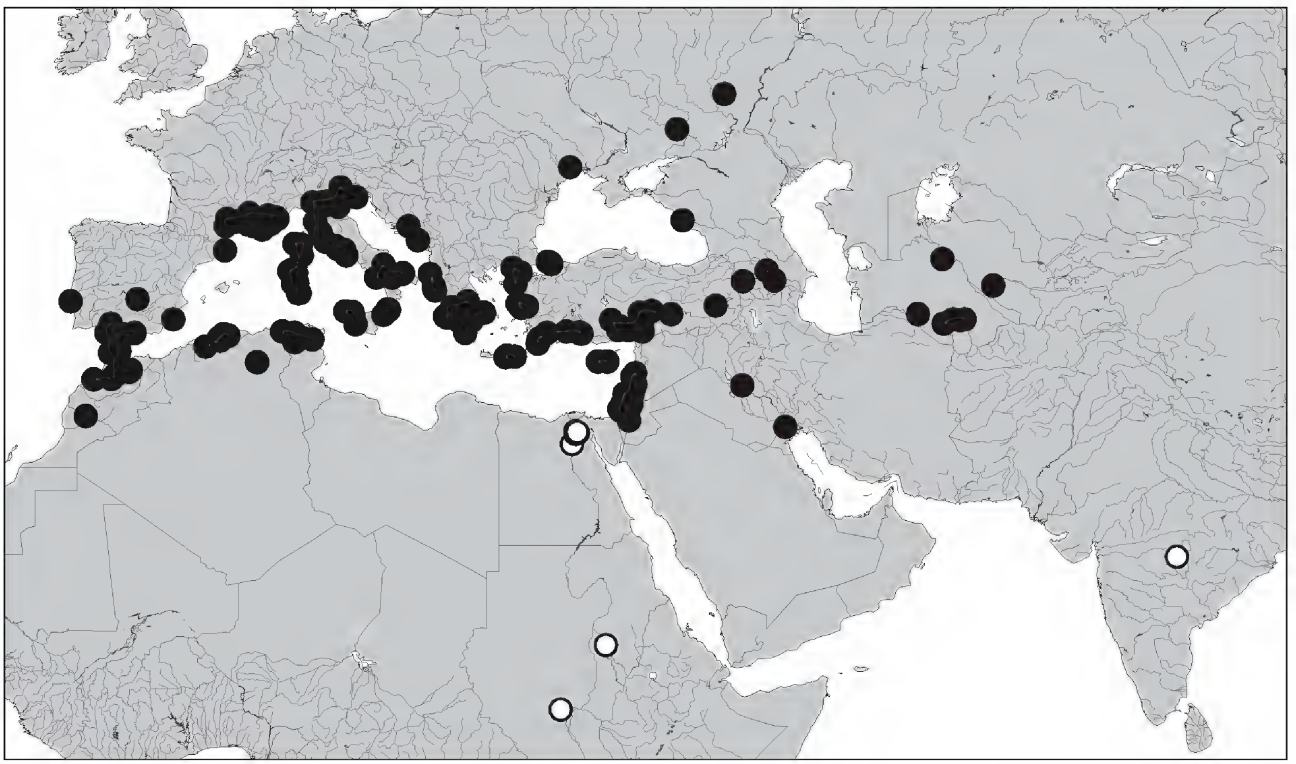


Fig. 2. Known distribution of the *Micrillus testaceus* species group (●) and the *M. aegyptiacus* group (○).

by Scheerpeltz (1962), the respective type localities being separated by more than 2000 km.

The *Micrillus* species treated here can be subdivided into two species groups, based on the morphology of the aedeagus, of the valvulae of the abdominal segment IX, and the morphology of the maxillary palpi. The first group, hereafter referred to as the *M. testaceus* group, is characterised by a rather simple aedeagal morphology with weakly sclerotised internal structures (see e. g. Figs. 16–26, 41–46), somewhat shorter valvulae of the abdominal segment IX, and a very long and slender apical maxillary palpomere. This group includes eight species (*M. testaceus*, *M. scabrosus*, *M. pallidus*, *M. irakensis*, *M. hypogaeus*, *M. subterraneus*, *M. biskrensis*, *M. tenuipennis*) and is confined to the south of the Western Palaearctic region, from the western Mediterranean to Middle Asia (Fig. 2). The highest diversity is in Northwest Africa (Morocco and Algeria), where the group is represented by six species, three of them distinctly microphthalmous and five of them with restricted distributions.

The representatives of the *M. aegyptiacus* species group are separated from those of the *M. testaceus* group by a complex and usually more or less asymmetric morphology of the aedeagus with distinctly sclerotised internal structures, remarkably long valvulae of the abdominal segment IX (except for *M. torretassoi*), and a shorter and somewhat conically shaped terminal maxillary palpomere. The *M. aegyptiacus* group currently includes four species (*M. aegyptiacus*, *M. torretassoi*, *M. sudanicus*, *M. indicus*). Two of the species (*M. aegyptiacus*, *M. torretassoi*) are distributed in the border zone between the Palaearctic and the Afrotropical regions, one (*M. sudanicus*) in the northeast of the Afrotropical region, and one (*M. indicus*) in the Oriental region (Fig. 2). It does not seem unlikely that at least some of the species currently attributed to *Scymbalium* from the Afrotropical and the Oriental regions (see e. g. Cameron 1931, Fagel 1960) may also belong to the *Micrillus aegyptiacus* group, but these species have not been revised. According to a catalogue excerpt by Herman (unpubl.), a total of 47 valid species of *Scymbalium* are currently known from the Afrotropical (21 species), Oriental (11 species), and Australian regions (15 species), in addition to the two Palaearctic species – *S. anale* (Nordmann, 1837) and *S. persimilis* Cameron, 1940 (holotype examined) – and the misplaced *S. minimum* Eppelsheim, 1888 (see section 3.5).

3.1.2 Ecology

Little is known about the ecological requirements of *Micrillus*. As can be inferred from the general distribution of the genus, especially from their absence from the temperate zones of the Palaearctic region, the species are apparently thermophilous. The examined material of the species of the *M. testaceus* group was mostly collected under stones in unforested habitats (agricultural land, grassland) at lower to intermediate altitudes. Occasionally winged specimens were collected in light traps or swept from the vegetation. The adaptive reductions of the eyes, hind wings, elytral length, and pigmentation in four North African species (*M. subterraneus*, *M. hypogaeus*, *M. tenuipennis*, and – to a lesser extent – *M. scabrosus*) suggest that they inhabit a subterranean habitat; according to the literature data and unpublished information made available by recent collectors, these species are typically found under large stones that are deeply embedded in the soil. While *M. pallidus* and *M. irakensis* are apparently fully winged, *M. testaceus* is wing-dimorphic, with the macropterous morph somewhat rarer than the brachypterous one. Both the rarity of records and the flat body suggest that they, too, predominantly dwell in subterranean crevices. *Micrillus biskrensis*, too, is apparently wing-dimorphic, but little is known about its distribution and its bionomics. As far as is currently known, species of *Micrillus* are univoltine.

The African representatives of the *M. aegyptiacus* group seem to be inhabitants of river banks, as is suggested by the data indicated on their labels and by the information provided in their descriptions. No information is available regarding the habitat of *M. indicus*.

3.1.3 Redescription

Species of intermediate size, 3.0–7.5 mm. Body more or less flattened.

Head of somewhat subquadrate shape, weakly oblong to weakly transverse. Antenna slender; antennomere I approximately as long as the combined length of II+III. Anterior margin of labrum incised in the middle, not dentate; maxillary and labial palpus slender, apical palpomere distinctly narrower than the preceding one, needle-shaped or weakly coniform. Neck approximately half the width of head.

Pronotum usually narrower than or approximately as wide as head and of somewhat trapezoid shape, widest near anterior angles and tapering posteriad; dorsal surface without distinct microsculpture; margins with long setae; midline impunctate.

Elytra with distinctly denser puncturation than head and pronotum; lateral margins with several long setae.

Legs slender; protarsus simple, undilated in both sexes; metatarsomere I approximately as long as the combined length of II+III.

Abdomen densely punctate. Valvulae of segment IX elongated in both sexes, distinctly projecting beyond posterior margin of tergite X; tergite X and sternite IX very small.

♂: sternite VII without distinct modifications; posterior margin of sternite VIII weakly to moderately excised in the middle; aedeagus without parameres.

3.1.4 Comparative notes

Among Palaearctic Paederinae, *Micrillus* is most similar to *Scymbalium*, which is represented in the Western Palaearctic region by only two species, *S. anale* and *S. persimile*. From this genus, *Micrillus* is distinguished by smaller body size, simple protarsi (in *Scymbalium* dilated in both sexes, in males more so than in females), a narrower neck (in *Scymbalium* about ⅔ the width of head), the finer puncturation of head and pronotum, the much longer valvulae of abdominal segment IX, the strongly reduced size of tergite X and sternite IX, and by the completely reduced parameres of the aedeagus (in *Scymbalium*, short parameres are present). For separation from other paederine genera occurring in the Palaearctic region see the key in Coiffait (1982).

3.2 The species of *Micrillus*

3.2.1 *Micrillus testaceus* (Erichson, 1840) (Figs. 3–33)

Scymbalium testaceum Erichson, 1840: 581.
Scymbalium grandiceps Jacquelin du Val, 1853: 699 f.; **resyn.**
Scymbalium longicolle Mulsant & Rey, 1853: 77 ff.
Scymbalium pubipenne Fairmaire, 1860: 159; **n. syn.**
Scymbalium longipenne Brisout de Barneville, 1863: 35 f.; **n. syn.** (previously a synonym of *S. pubipenne*).
Achenium saintpierrei Allard, 1869: 465 f.
Lithocharis trapezicollis Uhagón, 1876: 70 ff.
Schatzmayria meridionalis Gridelli, 1914: 70 f.; synonymy confirmed.
Schatzmayria tergestina Gridelli, 1914: 71; **n. syn.** (previously a synonym of *S. pubipenne*).
Scymbalium zuercheri Wanka, 1914: 141; **n. syn.**
Micrillus libanicus Coiffait, 1980: 150 f.; **n. syn.**
Micrillus hispanicus Coiffait, 1980: 151; **n. syn.**
Micrillus zacinthicus Coiffait, 1980: 151 f.; **n. syn.**
Micrillus syriacus Coiffait, 1980: 154; **n. syn.**
Micrillus calabricus Coiffait, 1980: 154; **n. syn.**
Micrillus turcicus Coiffait, 1980: 155; **n. syn.**
Micrillus graecus Coiffait, 1980: 155 f.; **n. syn.**
Micrillus cypriacus Coiffait, 1980: 156; **n. syn.**
Micrillus corcyranus Coiffait, 1980: 156 f.; **n. syn.**
Micrillus pubipennis var. *brevipennis* ["*pubipenne* var. *brevipenne*"]; Coiffait (1980: 157); unavailable name.
Micrillus brekhovi Grebennikov, 2001: 446 f.; **n. syn.**

Type material examined

S. testaceum: Lectotype ♂ [remounted], present designation: "6631 / *testaceum* Er., Sicil. SCHULTZ / Syntypus *Scymbalium testaceum* Erichson, 1840, labelled by MNHUB 2006 / Lectotypus ♂ *Scymbalium testaceum* Erichson desig. V. ASSING 2007 / *Micrillus testaceus* (Erichson) det. V. ASSING 2006" (MNHUB). – Paralectotype ♀: "Hist.-Coll. (Coleoptera), Nr. 6311, *Scimbalium* [sic] *testaceum* Erichs., 1840, Sicil., SCHULTZ, Zool. Mus. Berlin / Syntypus *Scymbalium testaceum* Erichson, 1840, labelled by MNHUB 2006 / Paralectotypus ♀ *Scymbalium testaceum* Erichson desig. V. ASSING 2007 / *Micrillus testaceus* (Erichson) det. V. ASSING 2006" (MNHUB).

S. meridionalis: Syntype [abdominal segments VIII and following missing]: "Lisbona, SCHATZMAYR / Typo / ♂ / *Schatzmayria meridionalis* Grid. det. GRIDELLI / Syntypus *Schatzmayria meridionalis* Gridelli rev. V. ASSING 2007 / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MCSNM).

S. tergestina: Holotype ♀ [macropterous]: "Noghera, 11.VI.911, SCHATZMAYR / *S. pubipenne* Fairm. / Holotypus ♀ *Schatzmayria tergestina* Gridelli rev. V. ASSING 2007 / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MCSNM).

S. zuercheri: Holotype ♀ [macropterous]: "Adana / coll. REITTER / Holotypus *Scimbalium Zürcheri* Wanka, 1914 [curator label] / *Scymbal. zürcheri* m. / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (HNHM).

M. calabricus: Holotype ♀: "Gerace, Calab. PAGANETTI / Holotype / *Micrillus calabricus* H. Coiffait det. 1980 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. corcyranus: Holotype ♂: "Corfou / Holotype / *Micrillus corcyranus* H. Coiffait 1979 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP). – Paratypes: 4 exs. [3 exs. macropterous]: "Paratype [curator label] / Corfu / G. C. CHAMPION B. M. 1927-409 / Paratype / *Micrillus graecus* Coiff. H. Coiffait det. 1971 / Paratypus *Micrillus corcyranus* Coiffait rev. V. ASSING 2007 / *Micrillus testaceus* det. V. ASSING 2007" (BMNH).

M. cypriacus: Holotype ♂: "Larnaka, Chypre, P. N. / Holotype / *Micrillus cypriacus* H. Coiffait 1980 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. graecus: Holotype ♀: "Attique / Holotype / *Micrillus graecus* H. Coiffait 1970 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP). – Paratypes: 2 ♀♀: same data as holotype (MNHNP); 1 ♀: "Grece / 82 / Museum Paris Coll. J. JARRIGE / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. hispanicus: Holotype ♀ [macropterous]: "Hispania, San Roque, Cadiz, J. VIVES leg. / Holotype / *Micrillus hispanicus* H. Coiffait 1979 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. libanicus: Holotype ♂ [macropterous]: "Liban, Joub Jannine, H. COIFFAIT, 16.XI.51 / Holotype / *Micrillus libanicus* H. Coiffait 1979 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. syriacus: Holotype ♂: "Dj. Cheik [= Mt. Hermon] / Holotype / *Micrillus syriacus* H. Coiffait 1980 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. turcicus: Holotype ♀: "[Locality illegible] Turq., VI.55. G. P. / Holotype / *Micrillus turcicus* H. Coiffait 1979 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. zacinthicus: Holotype ♂ [macropterous]: "Zante 1909, Kalámaki, legit O. HILF, Coll. O. LEONHARD / Holotype / *Micrillus zacinthicus* H. Coiffait 1980 / Muséum Paris / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (MNHNP).

M. brekhovi: Holotype ♂: "Volgogradskaya obl. Kalachevskiy r.-n. Naydenovskaya balka, 15.–23.VI.1990, O. G. BREKHOV 15–23.VI.1990 [collection data in Cyrillic] / *Achenium* sp. nova? CHATSCHIKOVE det. 1998 / Holotypus *Micrillus brekhovi* sp. n. K. GREBENNIKOV det. 2000 / Zoological Institute RAS St. Petersburg / *Micrillus testaceus* (Erichson) det. V. ASSING 2007" (ZIN).

Additional material examined
(total, including types: 492 exs. + 4 exs. of doubtful identity)

Tunisia: 2 exs., Aïn Draham, 27.–28.III.2003, leg. LACKNER (cAss); 1 ex., Aïn Draham, 2.V.2004, leg. LACKNER (cAss); 1 ex., Aïn Draham, XI.1945, leg. DEMOFLYS (cTro); 1 ex., Zaghouan, northern foot of Djebel Zaghouan, 30.XI.1994, leg. WRASE (cSch); 1 ex., Teboursouk [36°28'N, 9°15'E] (IRSNB); 1 ex. [macropterous], NE Jendouba, Bulla Regia [36°34'N, 8°48'E] (IRSNB); 1 ex. [macropterous], Le Kef, VI.1939, leg. NORMAND (cTro); 1 ex., Le Kef, X.1944, leg. NORMAND (cTro).

Algeria: 9 exs. [macropterous], Bône (DEI, IRSNB, cAss); 4 exs., Algier [macropterous] (BMNH, DEI); 1 ex. [macropterous], Biskra (MNHNP); 2 exs. [macropterous], locality not specified (BMNH, MNHNP).

Morocco: 1 ex. [macropterous], road Skirat to Sidi Bettache, 20 km NNW Sidi Bettache, 17.II.1999, leg. WRASE (cAss); 1 ex., Esmir [at the Mediterranean coast between Ceuta and Cabo Negro], leg. WALKER ["paratype" of *M. pubipennis* var. *brevipennis*] (MNHNP); 4 exs. [macropterous], Esmir, leg. WALKER (BMNH, IRSNB); 1 ex., Esmir (IRSNB, cAss); 1 ex., Moyen Atlas, Asni, 1200 m, 21.I.1990, leg. ARNDT (cAss); 1 ex., "Mellah", inundation, III.1963 (MHNG); 1 ex. [macropterous], Tetuan, leg. WALKER (cAss); 2 exs., Fedhala, 7.II.1935, leg. KOCH (MCSNM, cAss).

Gibraltar: 2 exs., "Gibraltar", leg. WALKER ["types" of *M. pubipennis* var. *brevipennis*] (MNHNP); 3 exs. [2 exs. macropterous], "Gibraltar", leg. WALKER (BMNH).

Spain: **Cataluña**: 1 ex., Gerona, Palamos, 7./13.IX.1974, leg. ULLBRICH (cAss). – **Castilla-La Mancha**: 4 exs., Pozuelo de Calatrava (NHMW, cAss). – **Murcia**: 1 ex., Cartagena, leg. SIMON (NHMW). – **Andalucía**: 2 exs., Cádiz, Tarifa, I.1997, leg. POOT (cAss); 2 exs., same data, but III.1991 (cAss, cWun); 1 ex., same data, but IV.1994 (cWun); 1 ex. [macropterous], same data, but I.1997 (cWun); 5 exs., Cádiz, 15 km N Jerez, Marisma de Trebujena, bank of Guadalqivir, 31.I.1998, leg. WRASE (cSch, cAss); 1 ex. [macropterous], Cádiz, Sanlúcar, 9.IV.1969, leg. COMELLINI (MHNG); 1 ex., Cádiz, Sierra de Luna, 350 m, stream bank, 28.III.1994, leg. WUNDERLE (cWun); 1 ex., Malaga, Velez de Malaga, 25.III.1998, leg. ESSER (cAss); 1 ex. [macropterous], Sevilla env., Los Palacios, leg. FRANZ (cAss); 1 ex. [macropterous], Sevilla env., Los Palacios, 7.IV.1959, leg. BESUCHET (IRSNB); 1 ex. [macropterous], Sevilla env., leg. FRANZ (cAss); 1 ex., Sierra de Ronda, 1800 m (NHMW); 1 ex., Algeciras, XI.–XII.1900, leg. CAMERON (BMNH); 1 ex., Algeciras, III.1901, leg. CAMERON (BMNH); 1 ex., San Roque, XI.–XII.1900, leg. CAMERON (BMNH); 1 ex., San Roque district, leg. CAMERON (BMNH); 1 ex., La Linea, III.1901, leg. CAMERON (BMNH); 1 ex., locality not specified, leg. SIMON (NHMW); 2 exs. [macropterous], locality not specified (DEI). – **Locality not specified**: 1 ex., "S. Spain", III.1901, leg. CAMERON (BMNH).

France: **Provence**: 3 exs., Nice env., flood debris, 22.II.1946, leg. COIFFAIT (MNHNP); 1 ex., Nice, 22.II.1967, leg. COIFFAIT (IRSNB); 1 ex., Hyères, 9.IV.1901 (MNHNP); 4 exs., Cannes (BMNH, DEI, IRSNB, MNHNP); 1 ex., Modène (IRSNB); 1 ex., Marseille (IRSNB); 1 ex., Fréjus (IRSNB); 1 ex. [macropterous], Saint-Raphael (IRSNB); 1 ex. [macropterous], Vaucluse, Angles (IRSNB); 2 exs., locality not specified (IRSNB). – **Languedoc-Rousillon**: 1 ex., Gard, Camargue, Pont des Tourradons [43°37'N, 4°16'E], 13.XI.1976, leg. CURTI (cAss); 1 ex.

[macropterous], same locality, 12.X.1994, leg. Lambelet (cTro); 1 ex., Béziers (IRSNB); 4 exs. [1 ex. macropterous], Lattes, leg. Lavagne (IRSNB); 1 ex. [macropterous], Lodève (IRSNB); 1 ex., Martigues, 24.IV.1934, leg. Tasso, Schatzmayr & Koch (MCSNM). – **Corse**: 2 exs. [1 ex. macropterous], Porto Vecchio (IRSNB); 2 exs., Porto, 26.V.1955, leg. Fagel (IRSNB); 7 exs. [2 exs. macropterous], locality not specified (HNHM, NHMW, cSch); 5 exs. [2 exs. macropterous], locality not specified, leg. Bauduer, Merkl (HNHM, NHMW).

Italy: **Emilia-Romagna**: 1 ex., Modena, San Cataldo, 1.VII.1896, leg. Fiori (NHMW); 3 exs., San Cataldo, 19.V.1895, leg. Fiori (SMF); 2 exs., San Cataldo (DEI, NHMW); 1 ex., Modena, 4.VI.1893, leg. Fiori (NHMW); 1 ex. [macropterous], Modena, 31.III.1895, leg. Fiori (SMF); 2 exs., Modena, 27.II.1897, leg. Fiori (MNHUB); 1 ex., Modena, 22.II.1882, leg. Fiori (MNHUB); 2 exs., Modena (NHMW); 1 ex. [macropterous], Galliera, 27.X.1910, leg. Fiori (MNHUB); 1 ex., Cagliata [?; first letter illegible], 21.V.1894, leg. Fiori (MNHUB); 1 ex. [teneral], S. Massa, 25.X.1896, leg. Fiori (MNHUB); 2 exs. [1 ex. macropterous], Bazzano, leg. Sekera (HNHM, SMTD); 1 ex. [macropterous], Ravenna, 8.IV.1964, leg. Collegar (MCSNM); 4 exs. [1 ex. macropterous], Parma, Felegara, 22.II.1976, leg. Rosa (MCSNM, cAss); 2 exs., Felegara, III.1976, leg. Rosa (MCSNM); 1 ex., Felegara, 2.XI.1978, leg. Pavesi (MCSNM); 1 ex. [macropterous], locality illegible, 8.V.1907, leg. Fiori (MNHUB); 2 exs., locality not specified (NHMW, SMF). – **Toscana**: 4 exs., Livorno, 18.VI.1886 (NHMW); 1 ex., Monte Argentario, leg. Moczarski (cAss); 1 ex., Follonica, IX.1962, leg. v. Breuning (MNHUB); 2 exs., locality not specified, leg. Bertolini, Stussiner (DEI, NHMW). – **Umbria**: 2 exs. [1 ex. macropterous], locality not specified (NHMW). – **Lazio**: 1 ex., Roma env. (MCSNM); 3 exs., Roma, Tolfa, 300 m, 14.II.1977, leg. Franzini (MCSNM); 1 ex. [macropterous], Latina, Cisterna, 27.X.1977, leg. Franzini (MCSNM); 1 ex., Roma env., locality illegible, 21.XII.1946 (MCSNM); 1 ex., Cerveteri, leg. Giaquinto (MCSNM); 1 ex., Aniene, leg. Porta (MCSNM). – **Basilicata**: 1 ex., Foresta di Accettura (MT), 21.III.1993, leg. Montemurro (cAss); 1 ex. [macropterous], Tursi (MT), 28.XII.1997, leg. Montemurro (cZan); 1 ex. [macropterous], Lavello, 1902, leg. Fiori (MNHUB). – **Campania**: 1 ex., Pattano (SA), 20.X.1966 (cZan). – **Calabria**: 5 exs., Antonimina, 1905, leg. Paganetti (DEI, NHMW, SMF, cAss); 1 ex., Melito di Porto Salvo, 6.XII.1975, leg. Curti (cSch); 4 exs., Aspromonte, Africo (RC), road to Samo, 100 m, meadow, 8.XI.1997, leg. Angelini (cAss, cZan); 7 exs., Aspromonte, San Luca (RC), 200 m, meadow, 24.I.2003, leg. Angelini (cAss, cZan); 3 exs., same data, but 23.I.2003 (cZan); 2 exs., San Luca, 8.XI.1997, leg. Montemurro (cZan); 1 ex., Roseto Capo Spulico (CS), 15.II.1998, leg. Montemurro (cZan); 1 ex., same data, but 28.XII.1997 (cZan). – **Puglia**: 3 exs., Taranto env., meadow, 16.XI.1997, leg. Angelini (cZan); 2 exs. [macropterous], Taranto env., 20.I.1997, leg. Montemurro (cAss, cZan); 1 ex., Porto Melitol, 10.XII.1975, leg. Curti (MHNG); 1 ex., Circum Mare Piccolo (TA), 24.XI.1976, leg. Montemurro (cZan); 1 ex., Taranto, Circum Mare Piccolo, 50 m, 22.II.1976, leg. Montemurro (MCSNM); 1 ex. [macropterous], same data, but 28.XI.1976 (MCSNM). – **Sardegna**: 1 ex. [macropterous], Cagliari, leg. Lostia (NHMW); 2 exs. [1 ex. macropterous], Cagliari, III.1883, leg. Dodero (IRSNB); 1 ex., Prov. Logoduro, Mores, leg. Gebhardt (NHMW); 6 exs., Asuni, leg. Krausse (MNHUB, cAss); 1 ex., Osilo, III.1961 (MHNG); 3 exs., Altopiano della Campeda, IV.1909, leg. Solari (MCSNM); 1 ex., Sassari, 5.XII.1975, leg. Franzini (MCSNM); 1 ex., Sassari, Marsa, 5.XII.1975, leg. Franzini (MCSNM); 1 ex., Assemini, leg. Lostia (MCSNM); 1 ex. [macropterous], Oristano, 5.V.1936, leg. Burlini (MCSNM); 5 exs. [1 ex. macropterous], locality not specified, leg. Lostia (DEI, MNHUB, NHMW); 1 ex., locality not specified (BMNH). – **Sicilia**: 1 ex., Ficuzza, 1906, leg. Leonhard (NHMW); 1 ex., Ficuzza, 15.II.1926, leg. Schatzmayr (MCSNM); 1 ex., San Vito lo Capo (TP), M. Sparagio, 2.XI.1991, leg. Sabella (cZan); 6 exs. [4 exs. macropterous], Palermo, leg. Rottenberg (DEI, cAss); 1 ex., Palermo (SMTD); 1 ex., Agrigento, Valle dei Templi, 4.III.1973, leg. Aliquò (MCSNM); 2 exs. [macropterous], locality not specified, leg. Rottenberg (DEI); 1 ex., locality not specified (IRSNB). – **Locality not specified or not identified**: 3 exs. (MNHUB); 1 ex., Larilo [?] Sasso, 20.XI.1917 (MCSNM).

Croatia: 3 exs. [1 ex. macropterous], "Istrien" (MNHUB, SMF).

Bosnia-Herzegovina: 2 exs. [macropterous], "Most. bl.", XI.1895, leg. Apfelbeck (NHMW).

Yugoslavia, Montenegro: 1 ex., Herzeg-Novi, leg. Paganetti (MNHUB); 1 ex., Herzeg-Novi, 3.V.1929, leg. Liebmann (DEI).

Albania: 3 exs. [macropterous], Vlorë ["Avlona"], leg. v. Oertzen (MNHUB, cAss).

Greece: **Greek mainland**: 13 exs., "Attica" (DEI, HNHM, MNHUB, NHMW); 1 ex., Fthiotis, SSE Lamia, Oros Kallidromo, 38°45'N, 22°28'E, 940 m, pasture, 2.IV.2001, leg. Wunderle (cWun); 2 exs., Aitolías-Akarnanías, Neochorion [38°25'N, 21°16'E], 1.V.1999, leg. Angelini (cWun); 1 ex., Nomós Évros, Évros delta, *Salicornia*, 22.IV.1994, leg. Bense (SMNS). – **Pelopónnisos**: 1 ex., Patras env., Mina, 900 m, 30.III.1986, leg. Assing (cAss); 3 exs., Patras, olive grove, 29.III.1986, leg. Assing (cAss, cWun); 1 ex., same data, but 26.III.1986 (cWun); 1 ex., Erimanthos, Hani Panopoulou, 600 m, 5.IV.1992, leg. Frisch (cAss); 1 ex., 7 km NW Andritsena, *Quercus coccifera* litter, 500 m, 3.X.2004, leg. Schawaller (SMNS); 1 ex., Nauplia (DEI); 1 ex., Kastanea, 8.IV.1981, leg. Tronquet (cTro); 1 ex., Koúmani ["Cumani"], leg. Brenske (HNHM). – **Kérkira (Corfu)**: 15 exs. [6 exs. macropterous], locality not specified, leg. Reitter, Sahlberg, etc. (DEI, HNHM, IRSNB, MNHUB, NHMW, SMF, SMNS, cAss); 1 ex. [macropterous], laguna (NHMW). – **Zákinthos**: 16 exs. [macropterous], Kalamaki, 1909, leg. Hilf (DEI, IRSNB, NHMW, SMF, SMTD, cAss); 1 ex. [macropterous], Limni Makry, 1936, leg. Hicker (NHMW); 1 ex. [macropterous], Limni Makry, 25.III.1936 (NHMW); 2 exs., locality not specified, 1909, leg. Leonhard (MNHUB). – **Kríti (Crete)**: 11 exs., Lasithi, Váï, palm beach, 21.III.1976, leg. Fülscher & Meybohm (MHNG, cAss, cWun); 2 exs., same data, but 27.III.1973 (MHNG); 1 ex., pass between Katharo and Lassithi, 1100 m, 16.IV.2000, leg. Meybohm (cAss); 1 ex., E-Crete, Neapolis, XI.1953, leg. Brondeel (IRSNB). – **Rhodos**: 1 ex., Lindos, Saidouras river, 18.IV.1994, leg. Frisch (cAss); 1 ex., Rhodos env., leg. v. Oertzen (MNHUB); 1 ex., Zambica, 20.II.1931, leg. Torre Tasso (MCSNM). – **Locality not specified**: 8 exs. [1 ex. macropterous], "Graecia" (DEI, NHMW).

Cyprus: 1 ex., Troodos mountains, Vretsia, 600 m, 10.III.1996, leg. Frisch (MNHUB); 6 exs. [1 ex. macropterous], locality not specified (DEI, IRSNB).

Turkey: **Istanbul**: 1 ex. [macropterous], "Belgrader Wald", leg. v. Bodemeyer (SMF); 1 ex., Alem Dağ, leg. v. Bodemeyer (SMF); 1 ex., Beykoz ["Beikos", 41°09'N, 29°05'E], IX.1903, leg. Cameron (BMNH); 1 ex., Beykoz, 1902, leg. Cameron (BMNH). – **Çanakkale**: 1 ex., 25 km S Kumkale, Beşik Koyu ["Besika Bay", ca. 39°49'N, 26°10'E], leg. Walker (BMNH); 2 exs., "Port Baklar" [ca. 40°33'N, 26°44'E], "Paratype [of *M. corcyranus*]" [leg. Walker] (MNHNP); 4 exs. [1 ex. macropterous], "Port Baklar", leg. Walker (BMNH). – **Izmir**: 6 exs., ca. 80 km NW Izmir, W Karaburun, 38°38'N, 26°29'E, 440 m, 4.IV.2006, leg. Anlaş, Assing, Wunderle (cAnl, cAss, cWun); 1 ex., "Vourlah Bay" [ca. 38°23'N, 26°47'E], leg. Walker (BMNH); 1 ex., Bornova, 31.VII.1931, leg. Uvarov (BMNH). – **Muğla**: 3 exs. [1 ex. macropterous], SE Dalaman, 36°47'N, 28°50'E, 10 m, floodplain forest, meadows, 28.III.2002, leg. Assing (cAss). – **Antalya**: 1 ex. [macropterous], road to Sak-

likent, 30 m, river bank, sweep-netting, 11.V.2000, leg. MEYBOHM (cAss); 1 ex. [macropterous], Manavgat env., Kızılot, 100 m, litter of oak and shrubs, 4.I.1991, leg. ASSING (cAss); 1 ex. [macropterous], Manavgat, VI.1989, leg. LUNDBERG (cWun); 1 ex. [macropterous], Manavgat, Side, VI.1989, at light, leg. LUNDBERG (cWun); 1 ex., Antalya-Kemer, 4.V.1975, leg. BESUCHET & LÖBL (MHNG). – **Konya**: 1 ex., 50 km S Beyşehir, Bakaran, 1400 m, under stones, 7.V.1978, leg. BESUCHET & LÖBL (cAss); 1 ex. [macropterous], 15 km NW Ereğli, Ereğli swamps, 1000 m, steppe and flood plain, 2.VI.1993, leg. SCHULZ (cAss). – **Mersin**: 1 ex., Çamlıyayla, 10.V.–3.VI.1963, leg. SCHUBERT (cAss); 1 ex., S Yeniköy, 1000–1200 m, 29.IV.1978, leg. BESUCHET & LÖBL (MHNG); 1 ex., locality not specified (MNHUB). – **Adana**: 2 exs., ca. 100 km SE Kayseri, 6 km W Küzükgezbeli, 1700 m, 10.V.1997, leg. SCHULZ, VOCK & SANETRA (cAss); 1 ex., Adana, 1906 (NHMW); 25 exs. [all macropterous], Adana, 4.VI.1934, leg. NEUBERT (MCSNM, NHMW). – **Osmaniye**: 4 exs. [macropterous], Osmaniye, 300 m, VI.1968, leg. SCHUBERT (cAss). – **Antakya**: 1 ex., Akbez (SMTD); 1 ex., ca. 10 km ENE Yayladağı, Güveççi, 29.IV.2007 (cAnl). – **Kahramanmaraş**: 2 exs., 50 km W Kahramanmaraş, 8 km SE Andırın, 37°35'N, 36°25'E, 1180 m, field margin, under stone, 19.III.2005, leg. ASSING, WUNDERLE (cAss, cWun); 1 ex., Elbistan, 26.V.–6.VI.1965, leg. SCHUBERT (cAss); 4 exs. [1 ex. macropterous], S Tekir, 900–1400 m, 5.V.1978, leg. BESUCHET & LÖBL (MHNG). – **Adıyaman**: 1 ex., Nemrut Dağı, 1800 m, 13.-15.V.1997, leg. SAMA (SMNS). – **Bitlis**: 1 ex., Tatvan, 1800 m, 1971, leg. SCHUBERT (NHMW). – **Locality not specified**: 1 ex. [macropterous], "Taurus Lyciae" (NHMW); 1 ex., "Turcia" (HNHM); 2 exs. [macropterous], "Asia min.", "Asia minor" (NHMW, SMF).

Lebanon: 1 ex., Laklouk [34°10'N, 35°53'E], 1500–1800 m, V.1964, leg. FAGEL (IRSNB); 2 exs. [macropterous], Nahr el Kelb, V.1964, leg. FAGEL (IRSNB).

Israel: 5 exs. [macropterous], Haifa, leg. SIMON (NHMW, cAss); 1 ex., Tel Aviv, 1.II.1978, leg. KAPLAN (TAU); 1 ex. [macropterous], 1 km W Hasolelim, 31.VII.2001, leg. ORBACH (TAU); 1 ex. [macropterous], N Oren, light trap, 4.VI.1999, leg. CHIKATUNOV & PAVLIČEK (cAss); 1 ex. [macropterous], Tel Kazir, 6.VIII.1956, leg. WAHRMAN (TAU); 1 ex. [macropterous], Nizzanim, 27.VII.1959, leg. GINZBURG (TAU); 2 exs. [macropterous], same data, but 24.VII.1959 (TAU); 1 ex. [macropterous], Nizzanim, 9.VI.1998, leg. FRIEDMAN (TAU); 1 ex. [macropterous], Ne'ot-HaKikkar, light trap, 16.VII.1999, leg. YAROM & KRAVCHENKO (TAU); 1 ex. [macropterous], Kokhav Ha Yarden, 29.VII.2002, leg. KRAVCHENKO & CHIKATUNOV (TAU); 1 ex. [macropterous], Hare Desle [?], 30.VI.1974, leg. KAPLAN (TAU); 1 ex. [macropterous], Merom Golan, Bental reservoir, 33°08'N, 35°47'E, 9.V.2006, leg. FRIEDMAN (TAU); 2 exs. [macropterous], Golan Heights, W Merom Golan, Bental reservoir, 1000 m, stony wetland near shore, 30.IV.2006, leg. WRASE (cSch, cAss); 1 ex. [macropterous], "Palaestina", leg. REITTER (HNHM).

Ukraine: 7 exs. [1 ex. macropterous], Odessa env., 8 km SSE Iljinka, right bank of Kuyalnik liman, opposite Protopopovka, under stones, 5.X.2001, leg. GONTARENKO (cGon, cAss); 2 exs. [1 ex. teneral], same data, but 6.X.2002 (cGon); 1 ex. [macropterous], same data, but 18.IV.2004 (cGon); 4 exs. [1 ex. macropterous], same data, but 17.VI.2004 (cGon, cAss); 1 ex. [macropterous], same data, but 15.VI.2004 (cAss).

Locality illegible or not indicated: 5 exs. [2 exs. macropterous] (IRSNB, MNHUB).

Identification doubtful [possibly referring to *M. pallidus*]: 1 ♀ [macropterous], Armenia, Verin Dzhrashen ["Aresch", 40°03'N, 44°30'E], leg. SCHELKOWNIKOV (NHMW); 1 ♀ [macropterous], Verin Dzhrashen (IRSNB); 1 ♀ [macropterous], Azerbaijan, Geok Tapa (IRSNB); 1 ♀ [teneral], Turkmenistan, "Dortkuju" [ca. 37°37'N, 61°14'E], V.1900, leg. HAUSER (NHMW).

Comments

All the examined type specimens were measured and the primary sexual characters of male holotypes were studied.

ERICHSON (1840) based the original description of *Scymbalium testaceum* on an unspecified number of syntypes collected in "Sicilia" by "Dom. Dr. SCHULTZ". Two syntypes – a male and a female, both brachypterous and of rufous coloration – were found in the historical collection at the MNHUB. The male is here designated as the lectotype.

The original description of *Scymbalium grandiceps* is based on two syntypes from the surroundings of Montpellier, southwestern France (JACQUELIN DU VAL 1853). The types were looked for, but not found at the MNHNP, where the collection of JACQUELIN DU VAL is deposited (HORN et al. 1990). However, the original description gives no evidence that it should not refer to a species of *Micrillus* and, since *M. testaceus* is the only species of the genus occurring in southern France, from where numerous specimens were examined, there is no doubt that the types are conspecific with *M. testaceus*. *Scymbalium grandiceps* was listed as a synonym of *M. testaceus* already by BERNHAUER & SCHUBERT (1912), but was later revalidated (COIFFAIT 1980, 1982; SMETANA 2004).

MULSANT & REY (1853) described *Scymbalium longicolle* based on an unspecified number of syntypes collected in "Hyères. Mars, Avril; sous les pierres, au bord des salines". The name was previously listed as a synonym of either *M. testaceus* or *M. grandiceps* (BERNHAUER & SCHUBERT 1912; COIFFAIT 1980, 1982; SMETANA 2004). The type material was not examined, but the original description leaves no doubt that it refers to *M. testaceus*, the only representative of the genus occurring in southern France.

Scymbalium pubipenne was originally described from an unspecified number of syntypes from "Bone", Algeria (FAIRMAIRE 1860). The type material was not found at the MNHNP, where the FAIRMAIRE collection is deposited (HORN et al. 1990). However, the original description leaves no doubt that it refers to *M. testaceus*, one of the two species of the genus with functioning eyes occurring in Algeria. Also, several specimens of *M. testaceus* collected in or near Bône were examined (see the following section).

The original description of *Scymbalium longipenne* is based on an unspecified number of syntypes from "Béziers", southern France (BRISOUT DE BARNEVILLE 1863). The type material was not found at the MNHNP, but it is doubtlessly conspecific with *M. testaceus*, as can be inferred from the original description and the fact that *M. testaceus* is the only species of the genus present in southern France. Previously, *S. longipenne* was regarded as a synonym of *M. pubipennis* (BERNHAUER & SCHUBERT 1912; SMETANA 2004).

The syntype material of *Achenium saintpierrei*, which was collected in "Oran" (Allard 1869), was not found in the collections of the MNHNP. The name has been regarded as a junior synonym of *M. testaceus* since the 19th century (Fauvel 1886; Bernhauer & Schubert 1912; Coiffait 1980, 1982; Smetana 2004). The original description gives no evidence that it should not refer to *M. testaceus*, whose distribution also includes Algeria, so that there is little doubt that the previously established synonymy is correct.

The original description of *Lithocharis trapezicollis* is based on four syntypes from the surroundings of Badajoz and Olivenza, Estremadura, Spain (Uhagón 1876). The type material was not found at the MNHNP, where, according to Horn et al. (1990), it should be deposited. The name was already treated as a synonym of *M. testaceus* by Bernhauer & Schubert (1912) and subsequent authors. *Micrillus testaceus* is the only representative of the genus present in Spain and the original description provides no evidence suggesting that the type specimens should not be conspecific with this species.

The original description of *Schatzmayria meridionalis* is based on two damaged syntypes, a male and a female, from "Lissabon (Portugal)" and an undamaged male syntype from "Gimino (Calabrien)" "in der Sammlung des Herrn Franz Tax in Graz" (Gridelli 1914). One of the damaged syntypes was found in the collections of the MCSNM; it is conspecific with *M. testaceus*. Since the abdominal apex including the aedeagus is missing and there is a chance that the syntype from the Tax collection may eventually become available, a lectotype designation is here refrained from.

Schatzmayria tergestina, whose original description is based on a single specimen from "Noghera bei Triest" (Gridelli 1914), was subsequently synonymised with *M. pubipennis* by Gridelli (1921). The holotype, a macropterous female of *M. testaceus*, was discovered among the non-type material from the MCSNM. Apparently, after becoming aware of the synonymy of *S. tergestina*, Gridelli removed the type label and replaced it with an identification label giving "*S. pubipenne* Fairm.".

Based on a single specimen ("Ein einzelnes Exemplar") from "Kleinasien (Adana)", Wanka (1914) described *Scymbalium zuercheri* ("*Scimbalium Zürcheri*"). The specimen is a macropterous female and conspecific with *M. testaceus*.

The original description of *M. calabricus* is based on a single female from "Italie, Calabre, Gerace, Paganetti leg." (Coiffait 1980). The specimen is a reddish coloured brachypterous specimen of *M. testaceus*.

The original description of *M. corcyranus* is based on a male holotype, as well as on four male and one female paratypes from "Corfou" (Coiffait 1980). Based on their external morphology and on the similar male sexual characters, the examined type specimens, including the holotype, are conspecific with *M. testaceus*. All of them are of dark coloration; three paratypes are macropterous. According to Coiffait (1980), the type material is deposited in his collection and in the collection of the British museum. Remarkably, the paratypes in the British museum were originally identified by Coiffait as *M. graecus*. It seems that he decided to describe *M. corcyranus* only after he had returned the specimens to London.

The original description of *M. cypriacus* is based on a single male from "Chypre, Larnaka" (Coiffait 1980). The brachypterous specimen was examined and both its external and its sexual characters leave no doubt that it is conspecific with *M. testaceus*.

Coiffait (1980) described *M. graecus* based on the female holotype and two female paratypes from "Grèce, Attique", as well as on one female paratype from "Grèce sans autre précision". In every respect, the type material is within the range of intraspecific variation of *M. testaceus*.

The female holotype of *M. hispanicus* is a dark-coloured macropterous specimen of *M. testaceus*.

The holotype of *M. libanicus* is a rather large dark macropterous male and doubtlessly conspecific with *M. testaceus*.

Micrillus syriacus was described from a single male from "Syrie, Hermon, Djebel Cheik" (Coiffait 1980). The holotype is a brachypterous specimen of *M. testaceus*.

The original description of *M. turcicus* is based on a single female from "Anatolie septentrionale: Trabzon" (Coiffait 1980). The locality written on the label, however, is illegible. The holotype doubtlessly refers to *M. testaceus*.

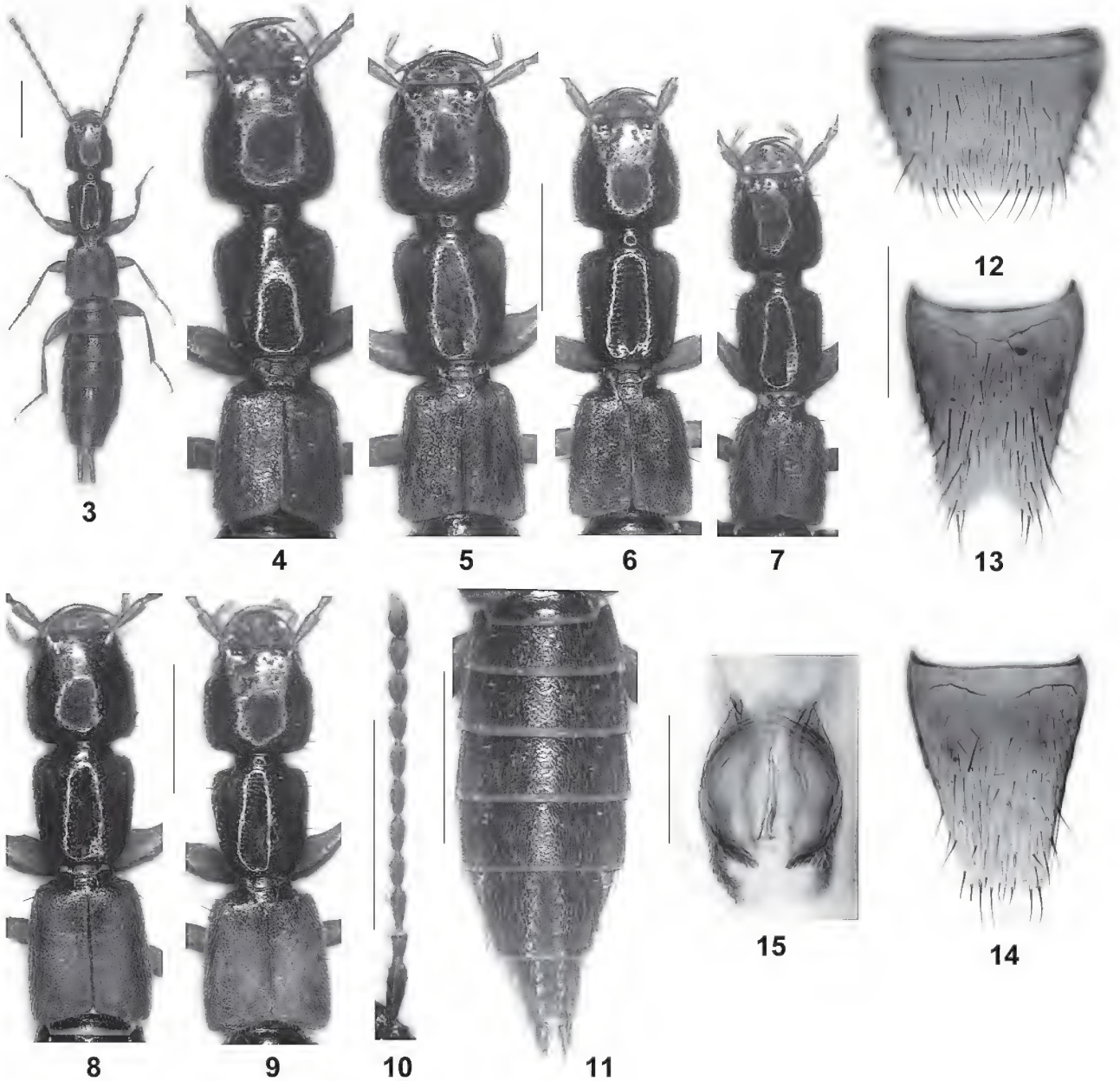
The holotype of *M. zacinthicus* is a macropterous male of *M. testaceus*.

According to Article 45.6.3 of the ICZN (1999), *M. pubipennis* var. *brevipennis* Coiffait, 1980 is not available. The "types" were studied and proved to refer to *M. testaceus*; the specimens are listed below as additional material (see Morocco and Gibraltar).

The original description of *M. brekhovi* is based on a single male from Volgograd province, Kalachevskiy district, south of Bolshaya Bolubaya river, Naydenova ravine [ca. 50°32'N, 42°59'E]. The brachypterous specimen is in every respect an average example of *M. testaceus*.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 330): AL: 1.68–2.68, 2.16; EyL (brachypterous morph): 0.10–0.20, 0.16; EyL (macropterous morph): 0.15–0.23, 0.19; POL (brachypterous morph): 0.36–0.60, 0.46; POL (macropterous morph): 0.33–0.56, 0.43; HL: 0.70–1.09, 0.88; HW: 0.69–1.09, 0.87; PW: 0.68–1.01, 0.81; PL: 0.74–1.09, 0.91; EL (brachypterous morph): 0.63–0.91,

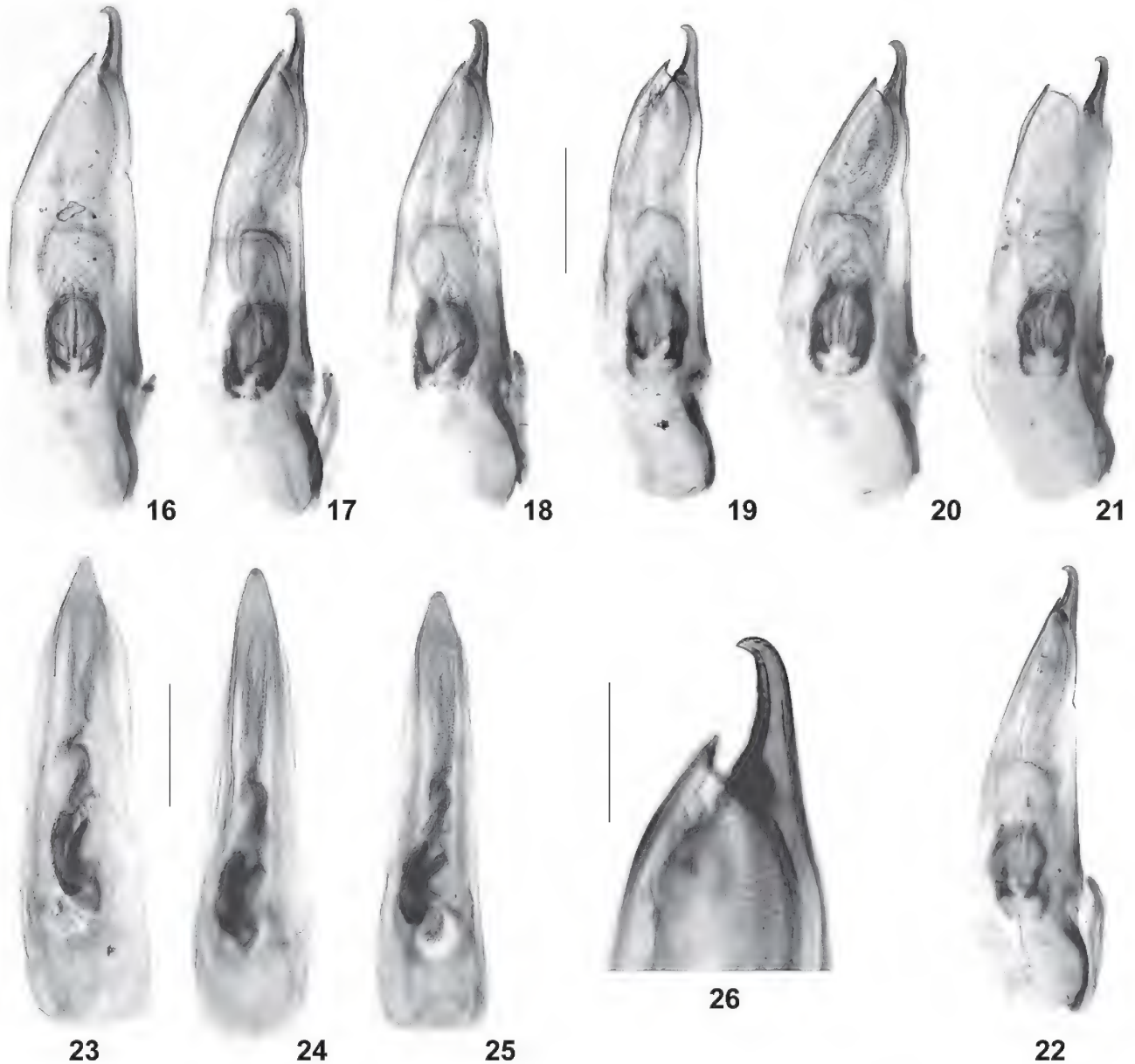


Figs. 3–15. *Micrillus testaceus* (Erichson). – **3**. Habitus. **4–9**. Forebody of brachypterous (4–7) and macropterous (8–9) specimens from Spain (4), Crete (5), Turkey (6–8), and Ukraine (9). **10**. Antenna. **11**. Abdomen. **12**. Male sternite VII. **13**. Male sternite VIII. **14**. Female sternite VIII. **15**. Internal structures of aedeagus. – Scale bars: 1.0 mm (3–11), 0.5 mm (12–14), 0.1 mm (15).

0.76; EL (macropterous morph): 0.76–1.03, 0.89; TiL: 0.65–1.03, 0.81; TaL: 0.54–0.88, 0.71; ML: 0.76–0.97, 0.84; TL: 4.2–6.9, 5.4; EyL/POL (brachypterous morph): 0.23–0.44, 0.34; EyL/POL (macropterous morph): 0.35–0.55, 0.44; HL/HW: 0.95–1.09, 1.01; PW/HW: 0.87–1.01, 0.94; PL/PW: 1.07–1.18, 1.12; EL/PL (brachypterous morph): 0.68–0.93, 0.83; EL/PL (macropterous morph): 0.91–1.06, 0.99; TiL/TaL: 1.02–1.33, 1.15.

Habitus as in Fig. 3. Highly variable species. Coloration variable, ranging from almost uniformly reddish or reddish brown to almost black with (usually) somewhat paler (dark reddish to brown) elytra and appendages; tarsomeres V almost always somewhat paler than I–IV.

Head of variable shape, weakly oblong to weakly transverse (see ratio HL/HW); posterior margin not distinctly concave in the middle; dorsal surface with usually



Figs. 16–26. *Micrillus testaceus* (Erichson). – **16–22**. Aedeagus of males from Spain (16–17), Italy (18–20), Turkey (21), and Greece (22) in lateral view. **23–25**. Aedeagus of males from Italy (23–24) and Greece (25) in ventral view. **26**. Apex of aedeagus in lateral view. – Scale bars: 0.2 mm (16–25), 0.1 mm (26).

distinct transverse microsculpture and with rather sparse punctures of variable size; interstices much wider than diameter of punctures (Figs. 4–9); eyes of variable size, larger in relation to postgenae and to body size in macropterous than in brachypterous specimens (see ratios EyL/POL). Antenna as in Fig. 10. Maxillary palpus slender, apical joint very long and slender, more than half the length of preapical joint and weakly conical.

Pronotum of variable shape and relative width, mostly somewhat narrower than head, but occasionally as wide as or even slightly wider than head (see ratio PW/HW); weakly to moderately oblong (see ratio PL/PW) and moderately tapering posteriad; posterior margin usually weakly concave, occasionally truncate; puncturation similar to that of head, but denser; along midline without punctures; microsculpture absent (Figs. 4–9).

Elytra of variable length, longer and more convex (cross-section) in macropterous (Figs. 8–9) than in brachypterous specimens (see measurements and ratio EL/PL), in brachypterous specimens usually more or less flat-

tened (Figs. 4–7) or even weakly impressed; humeral angles well marked, also in brachypterous specimens; puncturation dense, shallow, and irregular, sometimes weakly granulose; surface with weak shine; microsculpture present or absent. Hind wings dimorphic, either almost completely reduced or fully developed.

Legs of rather variable length (see measurements and ratio TiL/TaL); metatarsomere I approximately as long as the combined length of II+III or slightly shorter. Protarsi without sexual dimorphism.

Abdomen slightly wider than (brachypterous morph) to approximately as wide as elytra (macropterous morph), widest at segments V–VI; puncturation fine and very dense on tergites III–VI, slightly to distinctly less dense on tergites VII–VIII; interstices with shallow transverse microsculpture; posterior margin of tergite VII with palisade fringe (Fig. 11).

♂: sternite VII not distinctly modified, its posterior margin weakly concave (Fig. 12); sternite VIII posteriorly triangularly excised (Fig. 13); segments IX and X similar to those of *M. scabrosus* (cf. Fig. 40), valvulae of segment IX more than twice as long as tergite X; aedeagus of somewhat variable size (see measurements), weakly sclerotised, apically slender, acute (ventral view), and almost hook-shaped (lateral view) (Figs. 15–26).

♀: posterior margin of sternite VIII truncate (Fig. 14); segments IX and X similar to those of male.

Intraspecific variation

Maximum/minimum ratios: AL: 1.60; EyL (total): 2.38; EyL (brachypterous morph): 2.00; EyL (macropterous morph): 1.55; POL (total): 1.82; POL (brachypterous morph): 1.67; POL (macropterous morph): 1.68; HL: 1.55; HW: 1.57; PW: 1.49; PL: 1.44; EL (brachypterous morph): 1.43; EL (macropterous morph): 1.36; TiL: 1.58; TaL: 1.65; ML: 1.28; TL: 1.65; EyL/POL (brachypterous morph): 1.88; EyL/POL (macropterous morph): 1.57; HL/HW: 1.15; PW/HW: 1.17; PL/PW: 1.10; EL/PL (brachypterous morph): 1.36; EL/PL (macropterous morph): 1.17; TiL/TaL: 1.30.

Virtually all characters are subject to enormous intraspecific variation; this particularly applies to the coloration, all size-related parameters (see maximum/minimum ratios), and puncturation.

Specimens of predominantly reddish brown coloration were observed especially in material from southern Italy (including Sicilia) and Crete, whereas beetles from southern France, northern Italy, Greece (except Crete), and most parts of Turkey is mostly of dark coloration. Both colour morphs were observed in material from North Africa, certain regions of Italy (Emilia, Calabria, Sardinia), Spain, eastern Turkey (Adiyaman), and Israel. Macropterous specimens are usually of dark coloration.

In the material examined, 64.6% (312 exs.) of the specimens are brachypterous and 35.4% (171 exs.) are macropterous. The latter morph is present in the whole

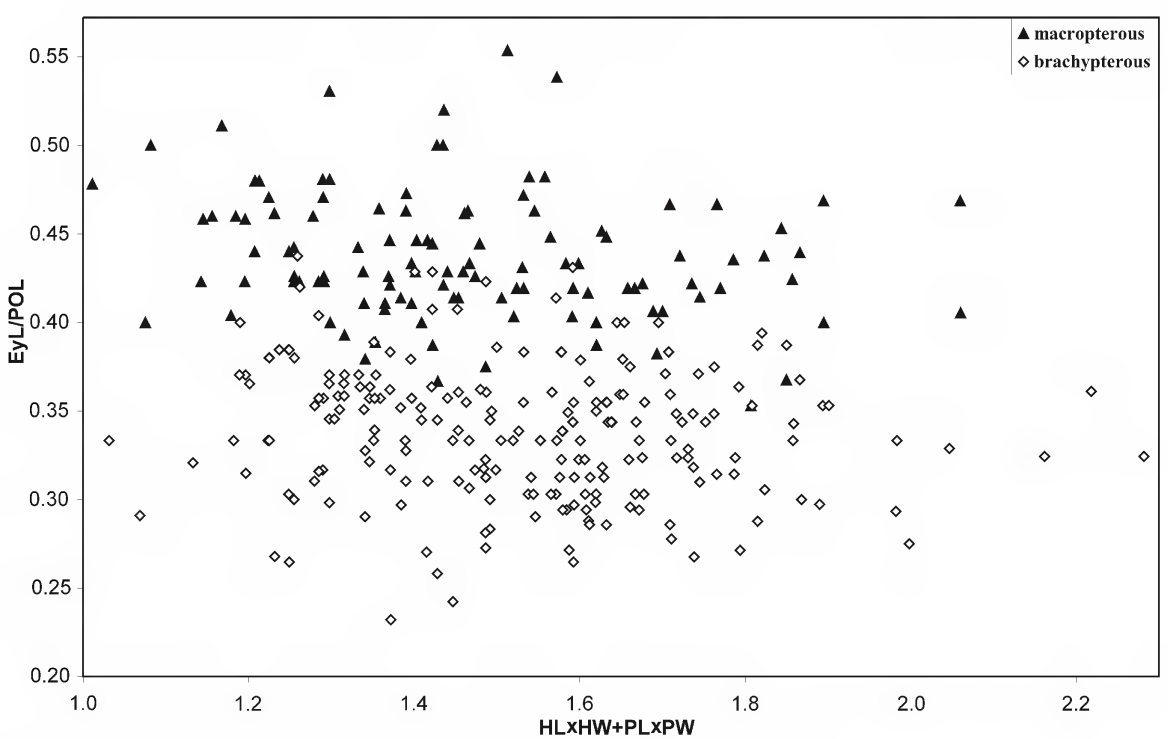


Fig. 27. *Micrillus testaceus* (Erichson). Relative eye size (EyL/POL) in relation to body size.

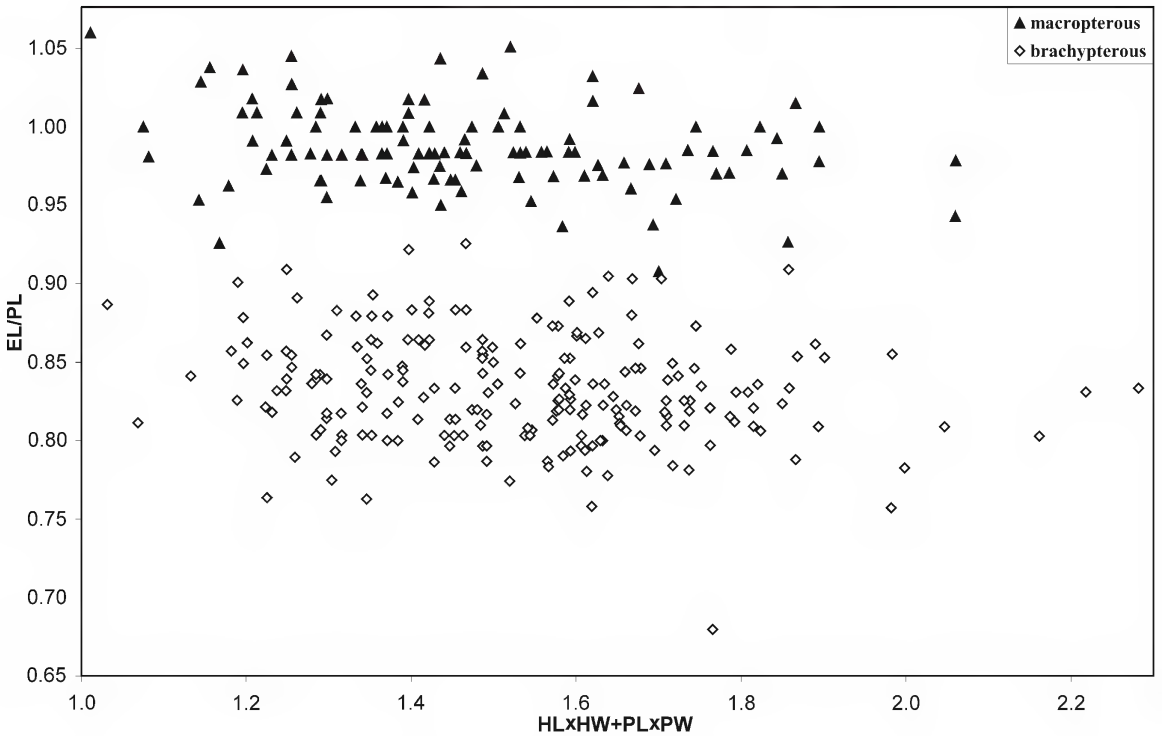


Fig. 28. *Micrillus testaceus* (Erichson). Relative elytral length (EL/PL) in relation to body size.

range of distribution, but was usually found less frequently than the brachypterous morph; the lowest proportion was observed in the material from Crete (all 18 specimens brachypterous). On the other hand, there are exceptions: the macropterous morph was predominant in the material from Algeria (16 macropterous/ 0 brachypterous), Morocco (6/4), Zakinthos (18/2), Turkey (41/34), Lebanon (2/1), and Israel (19/1). However, the possibility that these figures are – at least partly – due to a bias resulting from the application of certain sampling methods (e. g. light traps) cannot be ruled out.

Apart from the darker average coloration and the fully developed hind wings, the macropterous morph is distinguished from the brachypterous morph by smaller eyes (little overlap), as well as by less flattened and longer elytra (Figs. 4–8); both relative eye size and relative elytral length are independent of body size (Figs. 27–28).

Body size is extremely variable, but independent of wing development (Figs. 27–28). The largest specimens were observed in the material from Spain, whereas specimens from the Balkans are mostly closer to the lower end of the size range (Fig. 29).

Pronounced intraspecific variation was observed regarding the relative size of the head, which explains why this character is emphasised in the original descriptions of several of the junior synonyms of *M. testaceus*. The heads of specimens from the Balkans, southern France, and Italy are – on average – larger (in relation to body size), whereas those of material from Spain and North Africa tend to be smaller (Fig. 29).

Another character repeatedly referred to in the original descriptions is the shape of the head. As can be inferred from Fig. 30, however, no significant clinal trends can be observed, apart from the observation that heads of the specimens from Ukraine tend to be less slender than average. Generally, this character is highly variable in all parts of the range of the distribution.

Differences in the size of the aedeagus are mainly an expression of allometric variation (Fig. 31). The variability of the shape of the aedeagus is illustrated in Figs. 16–25.

Comparative notes

The species is distinguished from all its congeners especially by the morphology of the aedeagus, from the externally similar *M. pallidus*, *M. irakensis*, and *M. scabrosus* also by the usually darker coloration. A separation of pale-coloured macropterous females from *M. pallidus*, which is always macropterous, is generally difficult. From *M. irakensis*, however, *M. testaceus* is readily distinguished especially by the more or less truncate posterior margin of the head (in *M. irakensis* distinctly concave in the middle). For additional characters separating *M. testaceus* and *M. scabrosus* from northern Morocco, whose

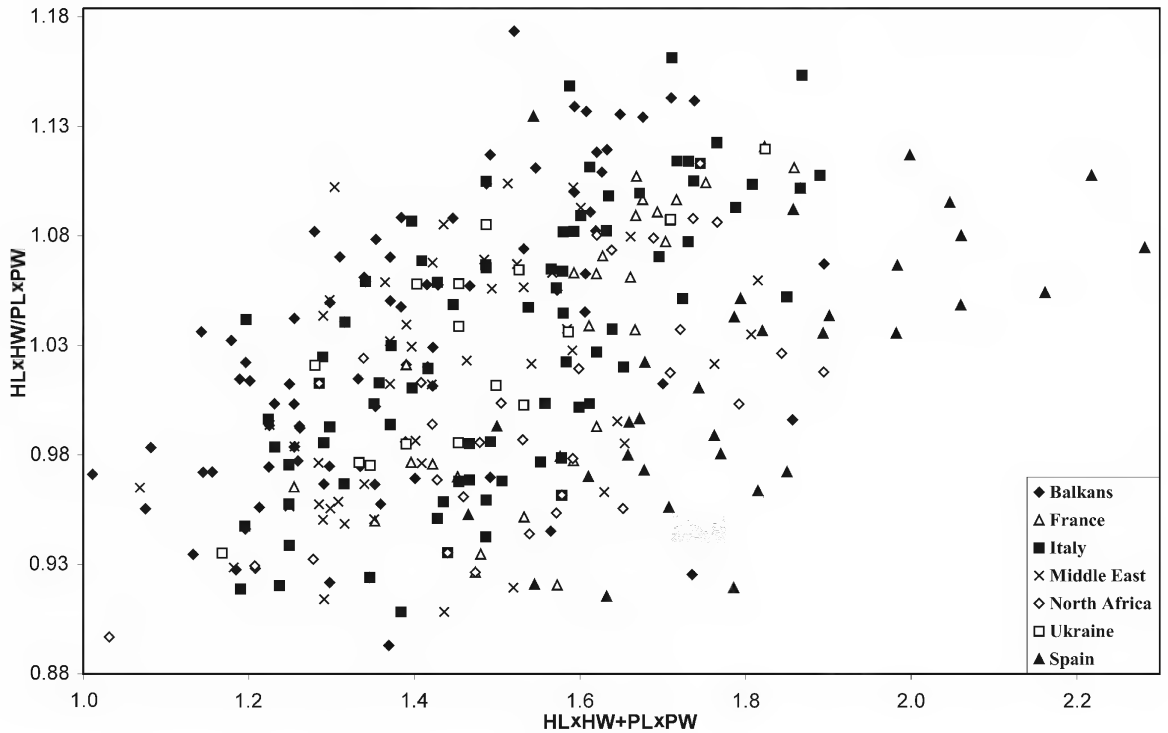


Fig. 29. *Micrillus testaceus* (Erichson). Relative head size in relation to body size (Spain: including Gibraltar; Middle East: including Turkey, Cyprus, Lebanon, Syria, Israel).

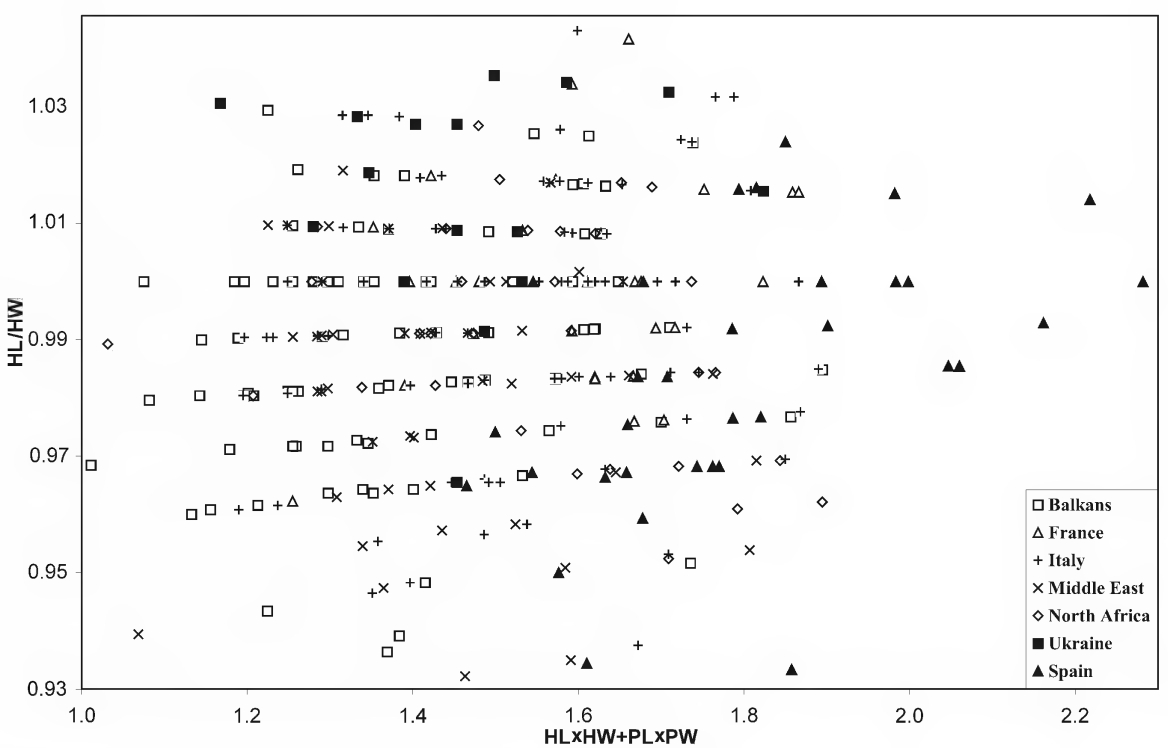


Fig. 30. *Micrillus testaceus* (Erichson). Head shape (HL/HW) in relation to body size (Spain: including Gibraltar; Middle East: including Turkey, Cyprus, Lebanon, Syria, Israel).

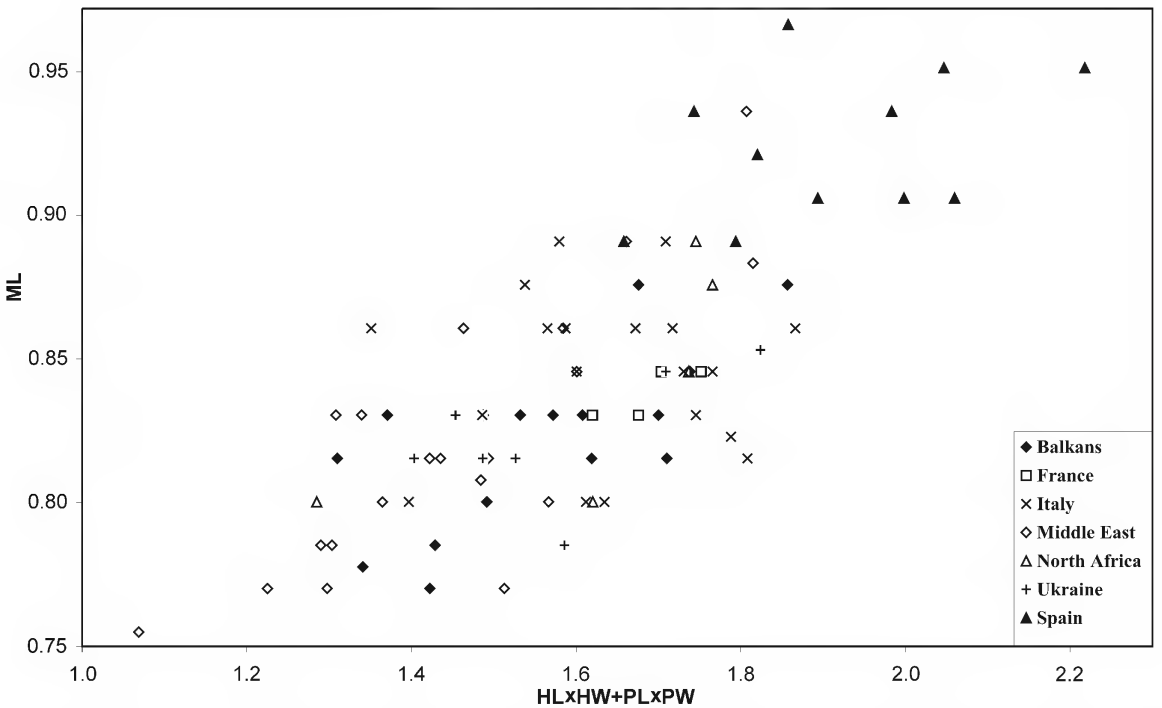


Fig. 31. *Micrillus testaceus* (Erichson). Length of aedeagus (ML) in relation to body size (Spain: including Gibraltar; Middle East: including Turkey, Cyprus, Lebanon, Syria, Israel).

aedeagus is somewhat similar, see the comparative notes in the following section.

Distribution and bionomics

M. testaceus is widespread in practically all of the Mediterranean region, its distribution extending to the northeast into Ukraine and the Russian South European territory (Fig. 32). According to Smetana (2004), the species (including all its synonyms) was previously unknown from Croatia, Bosnia-Herzegovina, Yugoslavia (Montenegro), and Israel.

Little is known about the habitat requirements. Most of the material either collected by the author or with specified data on the labels was found in unforested habitats such as pastures, meadows, field margins, floodplains, river banks (occasionally also in flood debris), partly also in saline habitats (beaches, *Salicornia* vegetation), and in habitats with scattered tree and shrub vegetation (olive and oak groves). The vast majority of specimens was found under stones. This, as well as the rarity of records and the flattened body suggest that the species primarily inhabits subterranean crevices. The altitudes range from 0–1800 m, but most of the records are apparently from lower and intermediate altitudes.

Adult beetles have been collected throughout the year, with the lowest number of records during summer (July–September) and a maximum in late winter and spring (Fig. 33). Teneral specimens were observed in October, suggesting that pre-imaginal development takes place in spring and summer. Based on the evidence available, dispersal by flight occurs in late spring and early summer. On several occasions, beetles were collected with light traps in June and July, and one macropterous specimen was swept from vegetation in May.

3.2.2 *Micrillus scabrosus* (Fauvel, 1875) (Figs. 34–47, 56–57)

Scymbalium scabrosum Fauvel, 1875: XXIII.

Type material examined

Lectotype ♂, here designated: "Tanger, inond. / *scabrosum* Fvl. / R. I. Sc. N. B. 17479 Coll. et det. A. Fauvel / Ex-Typis / Lectotypus ♂ *Scymbalium scabrosum* Fauvel desig. V. Assing 2007 / *Micrillus scabrosus* (Fauvel) det. V. Assing 2007" (IRSNB). – Paralectotypes: 2 ♀♀: same data as lectotype [on same pin as lectotype] (IRSNB); 1 ♀: same data as lectotype (IRSNB).

Additional material examined
(total, including types: 89 exs.)

Morocco: 11 exs., Tanger, Al-Hakkama, 35°38'N, 05°41'W, 100 m, arable land, 26.II.2004, leg. Assmann, Starke, Wrase (cAss, cFel, cSch); 1 ex., 35 km NW Meknès, Barrage d'El-Kansera, fallow land, 16.II.1999, leg. Wrase (cSch); 1 ex., Tétouan, ca. 4 km E Tétouan, debouchure of Oued Hajera, fields

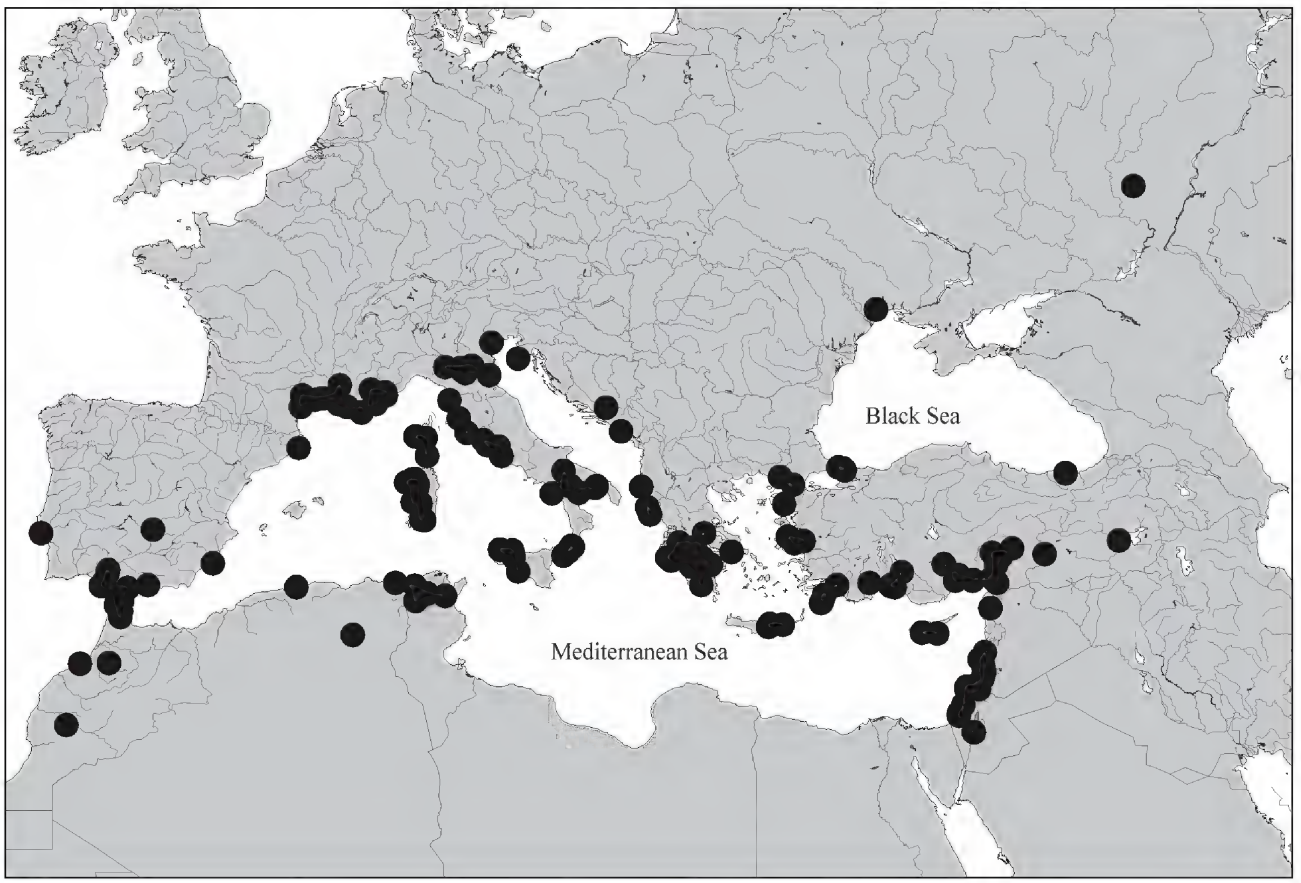


Fig. 32. *Micrillus testaceus* (Erichson). Distribution based on examined records; doubtful records are omitted.

and fallows, 15.II.2003, leg. Wrase (cSch); 1 ex., Tétouan (IRSNB); 4 exs., Cap Malabata, 28.XII.1977, leg. Minet (cTro); 1 ex., Arsila [35°28'N, 6°02'W] (HNHM); 22 exs., Tanger, leg. Escalera, Kraatz, Lewis, Quedenfeldt, Walker (BMNH, IRSNB, MNCN, MNHUB, NHMW); 30 exs., Tanger (BMNH, HNHM, IRSNB, MCSNM, MNCN, MNHUB, NHMW); 1 ex., Esmir (IRSNB); 12 exs., locality not specified (BMNH, IRSNB, NHMW).

Locality not indicated: 1 ex. (IRSNB).

Comments

The original description is based on an unspecified number of syntypes from "Tanger (Olcese)" (Fauvel 1875). Four syntypes, a male and three females were found in the Fauvel collection. The male is here designated as the lectotype.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 33): AL: 1.92–2.90, 2.67; EyL: 0.12–0.18, 0.15; POL: 0.47–0.68, 0.58; HL: 0.86–1.16, 1.05; HW: 0.85–1.18, 1.04; PW: 0.83–1.03, 0.96; PL: 0.90–1.14, 1.07; EL: 0.76–0.91, 0.83; TiL: 0.80–1.12, 1.02; TaL: 0.82–0.97, 0.90; ML: 0.76–0.83, 0.80; TL: 5.4–7.5, 6.5; EyL/POL: 0.21–0.33, 0.27; HL/HW: 0.97–1.05, 1.01; PW/HW: 0.87–1.00, 0.93; PL/PW: 1.07–1.16, 1.11; EL/PL: 0.72–0.89, 0.78; TiL/TaL: 1.08–1.19, 1.14.

Habitus as in Fig. 34. Coloration reddish to reddish brown, often with abdominal segments III–V or III–VI slightly infuscate; legs dark yellowish to yellowish brown, tarsomeres V usually pale yellowish; antennae rufous.

Head of somewhat variable shape, weakly oblong to weakly transverse (see ratio HL/HW); puncturation in lateral and posterior dorsal area rather coarse and dense, on average distinctly more so than in *M. testaceus*; middle of dorsal area with sparse and finer punctures, often almost impunctate (Fig. 35); whole surface with distinct microsculpture composed predominantly of transverse meshes; eyes on average smaller than in brachypterous *M. testaceus* (Fig. 38), weakly protruding from lateral contours of head in dorsal view. Antenna similar to that of *M. testaceus*, but longer (Fig. 36). Maxillary palpus of similar morphology as in *M. testaceus*, apical joint very long and slender, more than half the length of preapical joint and weakly conical (Fig. 39).

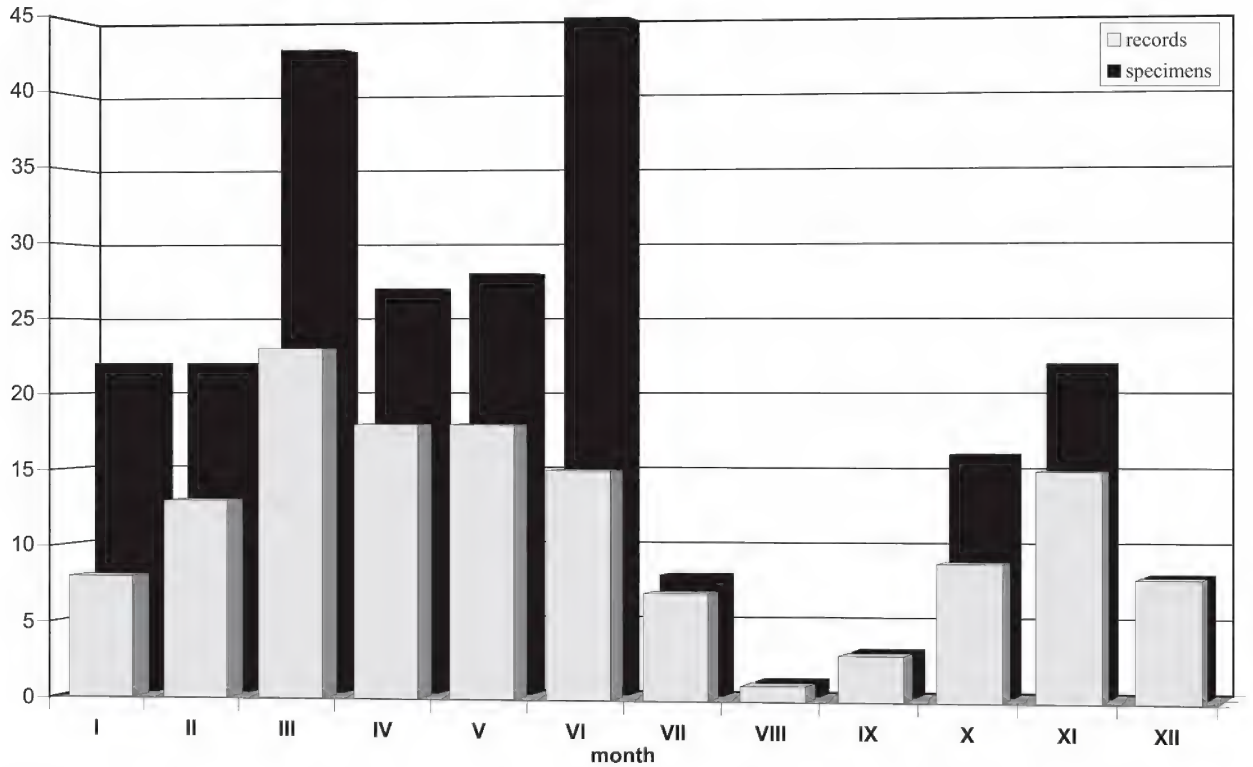


Fig. 33. *Micrillus testaceus* (Erichson). Seasonal distribution of the examined specimens (black bars) and samples/records (grey bars).

Pronotum as wide as head or slightly narrower, rather weakly oblong (see ratios PW/HW and PL/PW), and moderately tapering caudad; posterior margin truncate or weakly concave; puncturation rather dense and fine, much finer than that of head (Fig. 35); interstices on average approximately 1.5–2.0 times as wide as punctures; midline impunctate; microsculpture absent.

Elytra at suture distinctly shorter than pronotum (see ratio EL/PL and Fig. 35); dorsal surface somewhat depressed; puncturation conspicuously dense and moderately coarse, more so than that of pronotum, but finer than that of head; interstices on average as wide as punctures or narrower; microsculpture absent. Hind wings reduced.

Legs slender; metatarsomere I usually somewhat longer than the combined length of II+III, but shorter than the combined length of II–IV.

Abdomen approximately 1.2 times as wide as elytra, widest at segments V–VI; puncturation on tergites III–VI rather coarse, coarser than in *M. testaceus*, and somewhat granulose (Fig. 37); puncturation on tergites VII–VIII finer; interstices with microsculpture; posterior margin of tergite VII with narrow rudiment of a palisade fringe.

♂: sternite VII as in *M. testaceus*; posterior margin of sternite VIII shallowly triangularly excised (Fig. 56); segments IX and X similar to those of *M. testaceus*, valvulae of segment IX more than twice as long as tergite X (Fig. 40); aedeagus of similar morphology as in *M. testaceus*, but broader in ventral view, with more strongly sclerotised apex, and internal structures of slightly different shape (Figs. 41–46, 57).

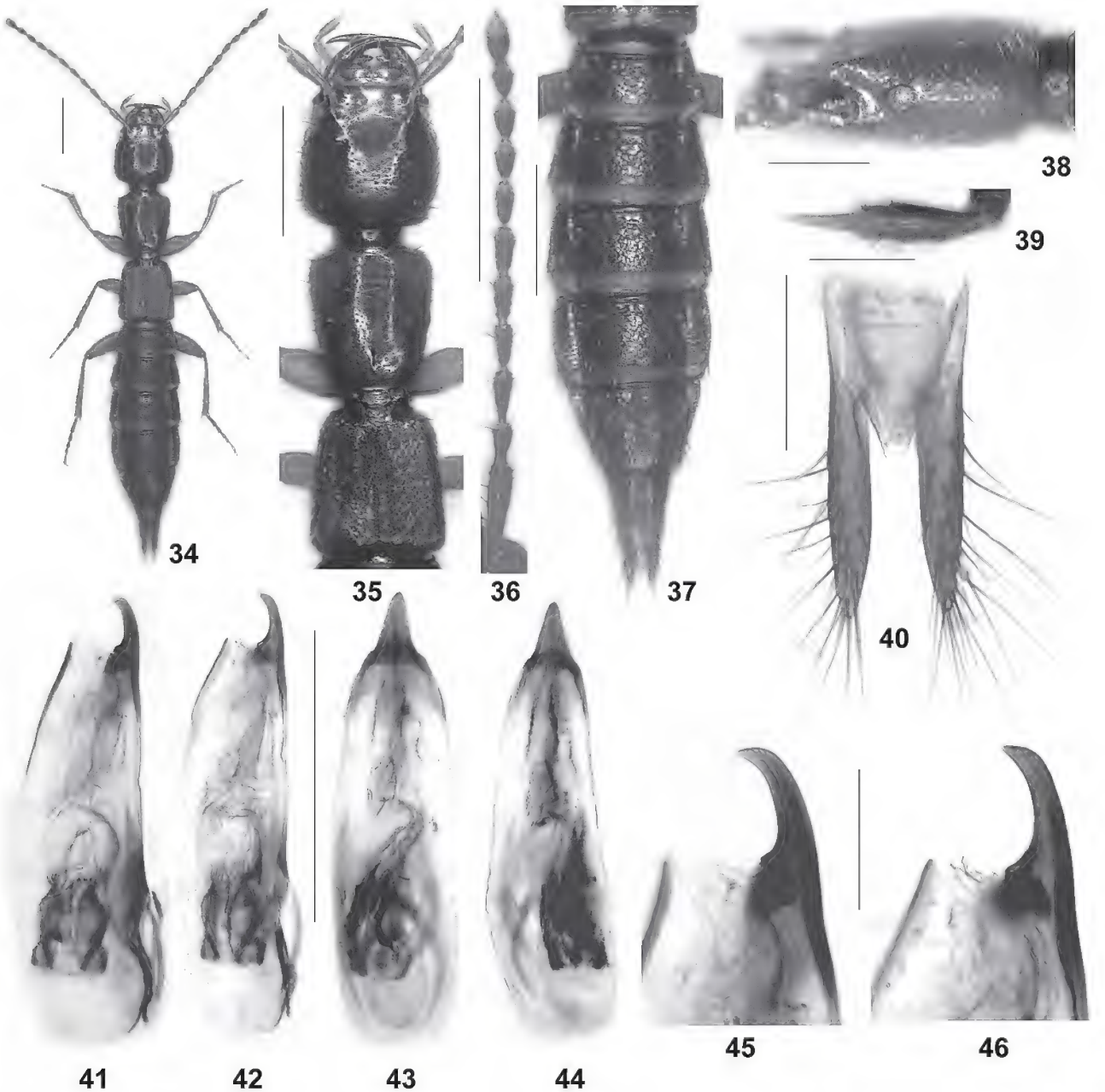
Intraspecific variation

Maximum/minimum ratios: AL: 1.51; EyL: 1.50; POL: 1.45; HL: 1.35; HW: 1.39; PW: 1.24; PL: 1.27; EL: 1.20; TiL: 1.40; TaL: 1.19; ML: 1.10; TL: 1.40; EyL/POL: 1.57; HL/HW: 1.08; PW/HW: 1.15; PL/PW: 1.08; EL/PL: 1.23; TiL/TaL: 1.11.

Especially the absolute and relative size of the eyes, the length of the antennae, and the length of the metatibiae are subject to pronounced intraspecific variation.

Comparative notes

Based on the highly similar morphology of the male primary and secondary sexual characters, as well as on external characters, there is little doubt that *M. scabrosus* is closely related to the variable *M. testaceus*, from which it is distinguished by larger average size, longer antennae, on average smaller eyes, coarser and – except for the elytra – denser puncturation of head, elytra, and abdomen, the



Figs. 34–46. *Micrillus scabrosus* (Fauvel). – **34**. Habitus. **35**. Forebody. **36**. Antenna. **37**. Abdomen. **38**. Head in lateral view. **39**. Apical palpomeres of maxillary palpus. **40**. Male abdominal segments IX–X. **41–44**. Aedeagus in lateral and ventral view. **45–46**. Apex of aedeagus in lateral view. – Scale bars: 1.0 mm (34–37), 0.5 mm (38, 40–44), 0.2 mm (39), 0.1 mm (45–46).

absence of a dimorphism of the elytra and the hind wings, the finer palisade fringe at the posterior margin of tergite VII, the less deep posterior incision of the male sternite VIII, as well as by the broader (ventral view) and apically more distinctly sclerotised aedeagus. From *M. tenuipennis*, the only other *Micrillus* species occurring in Morocco, it is readily distinguished by the presence of larger eyes with distinct ommatidia.

Distribution and bionomics

The species is endemic to northern Morocco (Fig. 47). The specimens with labels specifying ecological data were collected in arable land (fallows, fields) under stones. All the localities are situated at rather low elevations. The recently collected material was found in February and December. Fauvel (1902) also reports a record from January.

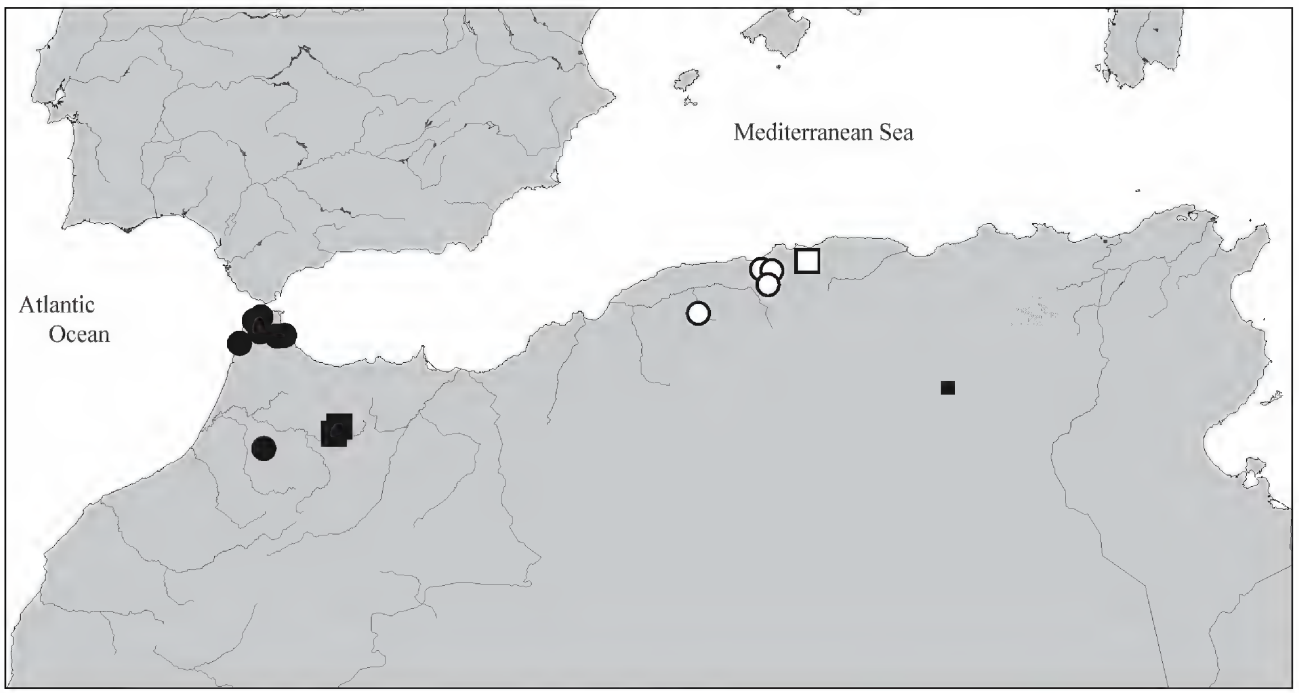


Fig. 47. Distributions of *Micrillus scabrosus* (Fauvel) (●), *M. subterraneus* Raffray (○), *M. hypogaeus* (Peyerimhoff) (□), *M. tenuipennis* n. sp. (■), and *M. biskrensis* (Fauvel) (■) in Northwest Africa, based on examined records.

3.2.3 *Micrillus pallidus* (Reitter, 1887) (Figs. 48–55, 58)

Scymbalium pallidum Reitter, 1887: 262.
Scymbalium rufotestaceum Cameron, 1939: 162; synonymy confirmed.
Micrillus caucasicus Coiffait, 1980: 152 ff.; **n. syn.**

Type material examined

S. pallidum: Holotype ♂ [dissected prior to present study]: "coll. Reitter / Monotypus [sic] *Scymbalium pallidum* Reitter, 1887 [curator label] / *Scimbalium pallidum* m. n. sp. Turcm. / Holotypus *Scimbalium pallidum* Reitter V. Gusarov rev. 1996 / *Micrillus pallidus* (Reitter) V. I. Gusarov det. 1995 / *Micrillus pallidus* (Reitter) det. V. Assing 2007" (HNHM).

S. rufotestaceum: Syntype ♀: "Cotype / Kiva [in Cyrillic] Pasar, 3.V. [collector in Cyrillic], C. Asia Khiva / *Scimbalium rufotestaceum* Cam. Cotype / = *pallidus* Reitt. comparé au type de *pallidus* H. Coiffait det. 1970 / *Micrillus pallidus* (Reitter) det. V. Assing 2007" (BMNH).

M. caucasicus: Holotype ♂: "Aresch, Caucasus, ex Schelkownikow / Holotype / *Micrillus caucasicus* H. Coiffait 1979 / Muséum Paris / *Micrillus pallidus* (Reitter) det. V. Assing 2007" (MNHNP). – Paratypes: 1 ♂, 1 ♀: "Aresch Caucase / Museum Paris Coll. J. Jarrige / Allotype [sic] / *Micrillus caucasicus* H. Coiffait 1979 / *Micrillus pallidus* (Reitter) det. V. Assing 2007" (MNHNP); 1 ♂: "Caucase Mesmm / *Scimbalium pallidum* / Paratype / *Micrillus caucasicus* H. Coiffait 1979 / *Micrillus pallidus* (Reitter) det. V. Assing 2007" (MNHNP).

Additional material examined
(total, including types: 131 exs.)

Armenia: 12 exs., Verin Dzhrashen ["Aresch"], leg. Schelkownikov (IRSNB, NHMW, cAss); 14 exs., Verin Dzhrashen (DEI, IRSNB, SMF, SMTD, cAss).

Azerbaijan: 1 ex., Geoktepe ["Gök-Tepe", 40°05'N, 46°58'E] (DEI); 1 ex., Geok Tapa [39°11'N, 48°41'E], leg. Schelkownikow (IRSNB); 6 exs., Geok Tapa (IRSNB); 3 exs., Gyandzha (= Kirovabad) ["Elisabethpol"] (NHMW).

Russian Federation: 1 ♀, Krasnodar, Uch-Dere ["Utsch-Dere", 43°40'N, 39°37'E] (NHMW).

Turkmenistan: 1 ex., Baïram-Ali [= Bayramaly], 11.–24.V.1959 (IRSNB); 3 exs., Mary ["Merw"], IV.1900, leg. Hauser (NHMW, cAss); 9 exs., "Dortkuju" [ca. 37°37'N, 61°14'E], IV.1900, leg. Hauser (DEI, MNHUB, NHMW, cAss); 3 exs., same data, but V.1900 (MNHUB, NHMW); 45 exs., Tedshen (IRSNB, MNHUB, cAss); 2 exs., Ashchabad, leg. Hauser (DEI, NHMW).

Uzbekistan: 1 ex., Buchara, leg. Hauser (NHMW).

Locality not specified or not identified: 16 exs., "Caucasus", "Caucas." etc. (DEI, IRSNB, SMF); 1 ex., "Tetschler, Transcasp." (SMF); 4 exs., "Transcaspia", leg. Aris (DEI); 2 exs. (IRSNB).

Comments

Some of the material of *S. pallidum* in the Fauvel collection at the IRSNB is labelled "Ex-Typis". However, since the original description of *S. pallidum* is based on a

single specimen ("ein einzelnes Exemplar") from "Turcmenien" (Reitter 1887), they do not have type status.

Cameron (1939) based the original description of *Scymbalium rufotestaceum* on an unspecified number of syntypes from "Khiva (Zimin)", only one of which was found in the Cameron collection. Since it is a female, it is not designated as the lectotype. The synonymy of *S. rufotestaceum* with *Micrillus pallidus* is here confirmed.

The original description of *M. caucasicus* is based on a male holotype and two female paratypes from "Caucase, Aresh", a male paratype from "Caucase (sans autre précision)", and a female paratype from "Transcaucasie, Geok Tapa" (Coiffait 1980). An examination of the holotype and three paratypes yielded no evidence whatsoever that they should be specifically distinct from *M. pallidus*. On the contrary, they represent rather average examples of the species. Consequently, *M. caucasicus* Coiffait is here placed in the synonymy of the senior name *M. pallidus*.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 17): AL: 1.77–2.04, 1.91; EyL: 0.13–0.20, 0.17; POL: 0.33–0.45, 0.39; HL: 0.71–0.85, 0.79; HW: 0.65–0.82, 0.75; PW: 0.63–0.76, 0.70; PL: 0.77–0.89, 0.84; EL: 0.72–0.85, 0.78; TiL: 0.66–0.79, 0.72; TaL: 0.59–0.68, 0.63; ML: 0.60–0.68, 0.63; TL: 4.2–5.3, 4.7; EyL/POL: 0.37–0.55, 0.44; HL/HW: 1.01–1.09, 1.05; PW/HW: 0.91–1.00, 0.94; PL/PW: 1.15–1.22, 1.19; EL/PL: 0.91–0.98, 0.94; TiL/TaL: 1.09–1.17, 1.13.

Coloration almost uniformly yellowish to reddish yellow, with the appendages and the elytra pale yellowish.

Head weakly oblong (see ratio HL/HW and Figs. 48–49), of similar shape, puncturation, and microsculpture as in *M. testaceus*; posterior margin not distinctly concave; eyes approximately of similar relative size as in the macropterous morph of *M. testaceus*. Antenna and maxillary palpus as in *M. testaceus*.

Pronotum slightly narrower than head and distinctly oblong (see ratios PW/HW and PL/PW), weakly tapering posteriad (Figs. 48–49); posterior margin truncate or weakly concave in the middle; puncturation finer and distinctly denser than that of head; microsculpture absent.

Elytra at suture slightly shorter than pronotum (see ratio EL/PL); humeral angles pronounced; puncturation fine and dense (Figs. 48–49). Hind wings fully developed.

Legs of similar morphology as in *M. testaceus*.

Abdomen approximately as wide as or slightly wider than elytra, widest at segments V–VI; puncturation very fine and extremely dense, slightly less dense on tergites VII and VIII than on anterior tergites; interstices with microsculpture; posterior margin of tergite VII with palisade fringe.

♂: sternite VII as in *M. testaceus*; posterior margin of sternite VIII broadly and shallowly concave (Fig. 50); aedeagus of distinctive shape and with two sets of sclerotised internal structures of characteristic morphology (Figs. 51–55).

Intraspecific variation

Maximum/minimum ratios: AL: 1.16; EyL: 1.53; POL: 1.36; HL: 1.19; HW: 1.27; PW: 1.19; PL: 1.16; EL: 1.17; TiL: 1.18; TaL: 1.15; ML: 1.13; TL: 1.26; EyL/POL: 1.49; HL/HW: 1.08; PW/HW: 1.10; PL/PW: 1.06; EL/PL: 1.08; TiL/TaL: 1.07.

Except for the highly variable relative and absolute eye size, morphological characters are subject to moderate intraspecific variation.

Comparative notes

Micrillus pallidus is readily separated from its congeners based on the distinctive morphology of the aedeagus, whose ventral process is not bent dorsad in lateral view. From other species of the *M. testaceus* group with fully developed hind wings and eyes of normal size, it is additionally distinguished as follows:

from *M. testaceus* by smaller average size, paler coloration, and the shallow excision of the posterior margin of the male sternite VIII;

from *M. irakensis* by the truncate or – at most – weakly concave posterior margin of the head (in *M. irakensis* distinctly concave).

A reliable separation from teneral macropterous females of *M. testaceus* based on morphogical characters may prove difficult.

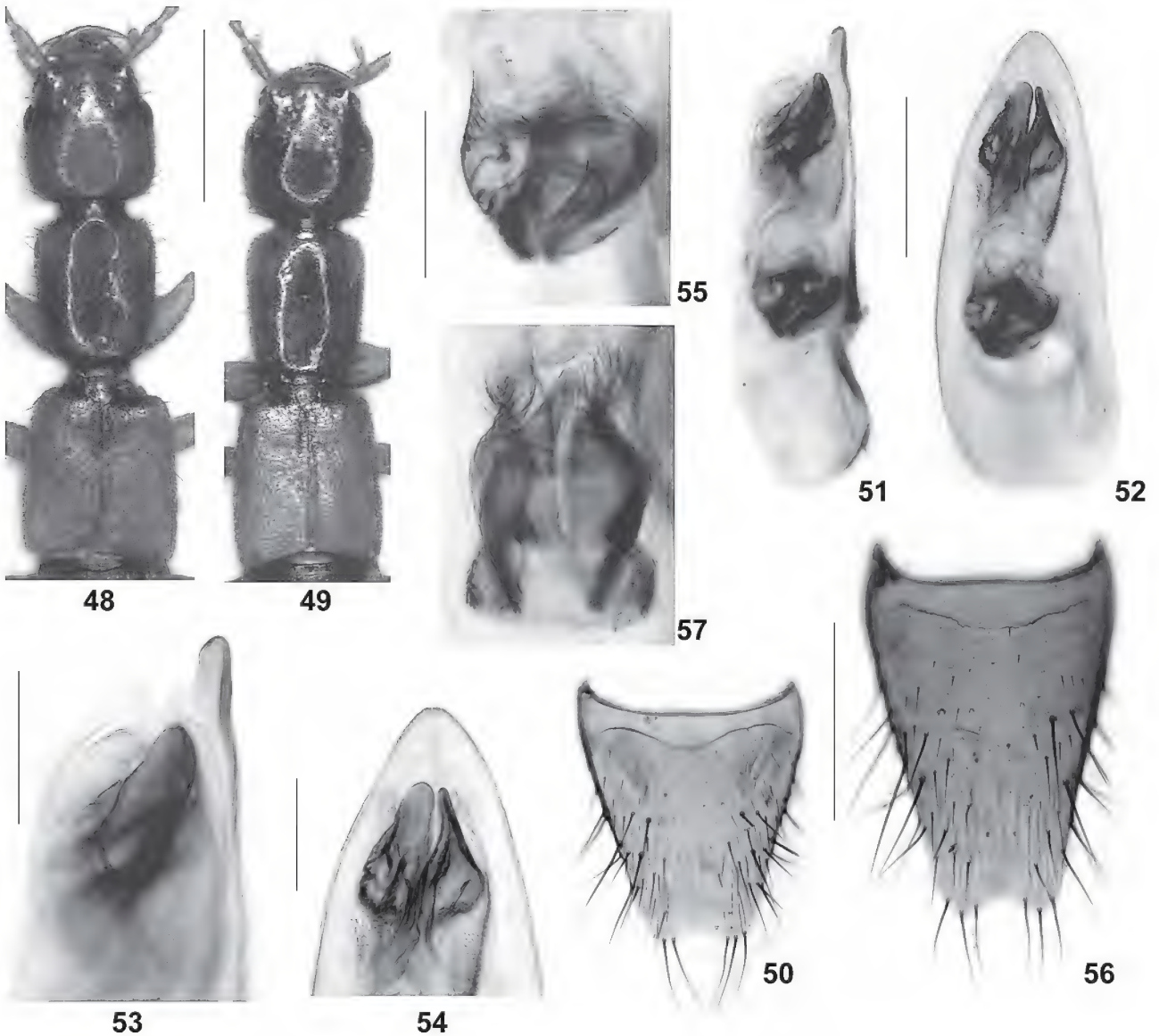
Distribution and bionomics

The currently known distribution includes the Caucasus region (Russian South European territory, Armenia, Azerbaijan) and Middle Asia (Turkmenistan, Uzbekistan) (Fig. 58). According to Smetana (2004), the species was previously unknown from the Russian Federation and Azerbaijan. Gusarov (1989) reports it (as *M. caucasicus*) from Ukraine (Crimea) – a record omitted in Smetana (2004) –, but in view of the frequent confusion of *Micrillus* species, this record should be considered doubtful until males from this region become available for revision.

Most of the material examined was collected a long time ago, so that hardly any bionomic information is provided on the labels, apart from the fact that some specimens were taken in April and May.

3.2.4 *Micrillus irakensis* (Cameron, 1940) (Figs. 58–74)

Scimbalium (Schatzmayria) irakense Cameron, 1940: 251.



Figs. 48–57. *Micrillus pallidus* (Reitter) (48–55) and *M. scabrosus* (Fauvel) (56–57). – **48–49**. Forebody of specimens from Armenia (48) and Turkmenistan (49). **50**, **56**. Male sternite VIII. **51–52**. Aedeagus in lateral and ventral view. **53–54**. Apex of aedeagus in lateral and ventral view. **55**, **57**. Internal structures of aedeagus. – Scale bars: 1.0 mm (48–49), 0.5 mm (50, 56), 0.2 mm (51–52), 0.1 mm (53–54, 55, 57).

Type material examined

Holotype ♀: "Bag [reverse side of mounting label] / Holotype [curator label] / *S. irakense* Cam. Type / M. Cameron. Bequest B. M. 1955-147 / Holotype *Scimbalium irakense* Cameron, 1940 det. R. G. Booth 2007 / Holotypus *Scymbalium irakense* Cameron rev. V. Assing 2007 / *Micrillus irakensis* (Cameron) det. V. Assing 2007" (BMNH).

Additional material examined
(total, including type: 10 exs.)

Iraq: 1 ex., Baghdad env., VI.1932, leg. Vanderjist (NHMW); 3 exs., Baghdad (IRSNB, cAss); 1 ex., NE Basra, At Tannūmah ["Tanooma"] (BMNH); 1 ex., "Mesopot." (MNHUB); 1 ex., "Mesopotamia" (MNHNP).

Israel: 1 ex., Jericho, at light source, 8.VII.1929, leg. Tapukhi (BMNH); 1 ex., "Palestine, Jordan", 17.VIII.1939, leg. "Bytinski-Salz" (TAU).

Comment

The original description is explicitly based on a single type specimen from "Baghdad" (Cameron 1940).

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 7): AL: 1.92–2.14, 2.03; EyL: 0.21–0.23, 0.22; POL: 0.33–0.38, 0.35; HL: 0.72–0.77, 0.74; HW: 0.74–0.80,

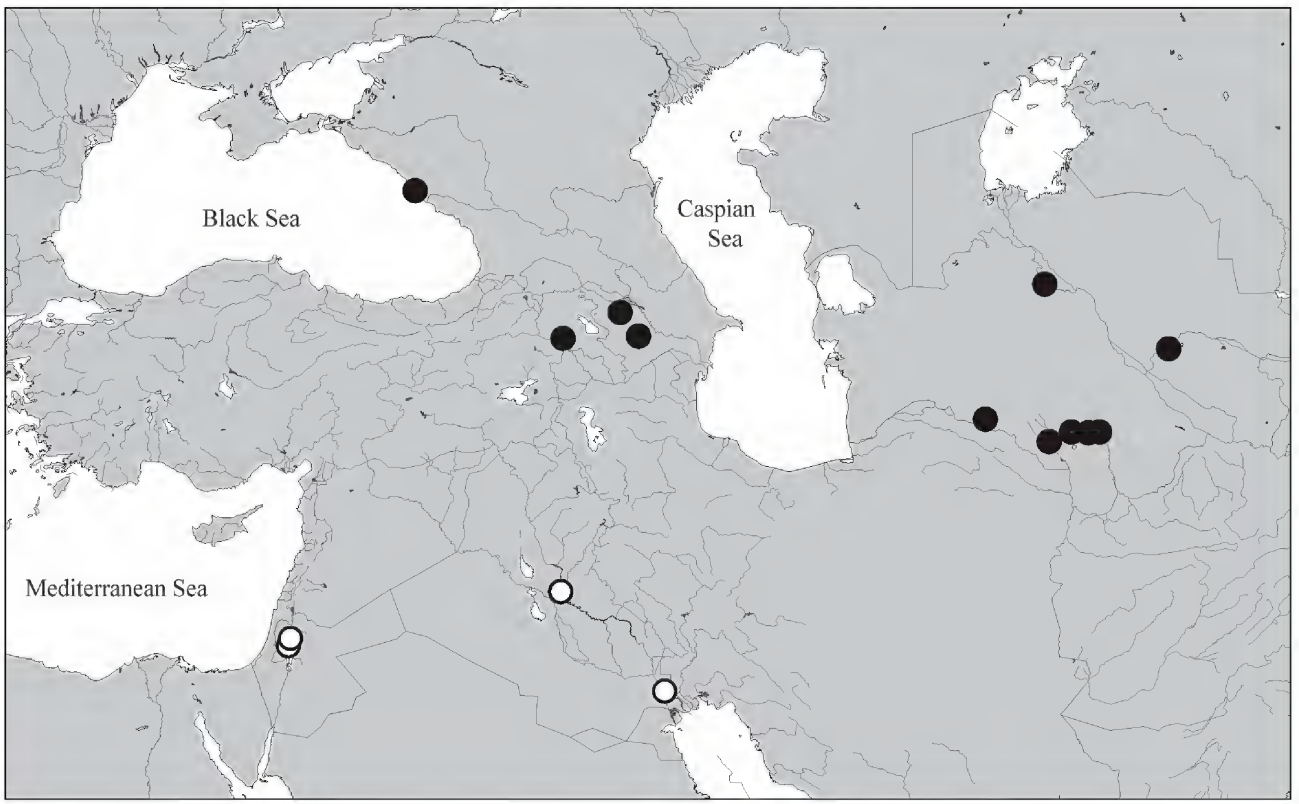


Fig. 58. Distributions of *Micrillus pallidus* (Reitter) (●) and *M. irakensis* (Cameron) (○), based on examined records.

0.76; PW: 0.71–0.79, 0.74; PL: 0.79–0.88, 0.84; EL: 0.76–0.91, 0.84; TiL: 0.60–0.74, 0.71; TaL: 0.62–0.66, 0.64; ML: 0.62; TL: 4.7–5.6, 5.1; EyL/POL: 0.58–0.68, 0.63; HL/HW: 0.95–0.98, 0.97; PW/HW: 0.95–0.98, 0.97; PL/PW: 1.11–1.17, 1.14; EL/PL: 0.96–1.04, 1.00; TiL/TaL: 1.10–1.15, 1.12.

Habitus as in Fig. 59. Coloration: head and pronotum yellowish to brown; elytra yellowish to yellowish brown; legs and antennae yellowish to yellowish brown.

Head weakly transverse (see ratio HL/HW); posterior margin conspicuously concave (Figs. 60–61); puncturation moderately fine and sparse, interstices distinctly wider than diameter of punctures; surface glossy, with very shallow transverse microsculpture; eyes large (see measurements, ratio EyL/POL, and Fig. 62) and distinctly projecting from lateral contours of head. Antenna similar to that of *M. testaceus* (Fig. 63); maxillary palpus slender, apical palpomere approximately half the length of preapical palpomere or slightly longer.

Pronotum slightly narrower than head, distinctly oblong (see ratios PW/HW and PL/PW), and weakly tapering caudad; puncturation finer and denser than that of head; midline impunctate (Figs. 60–61).

Elytra approximately 1.25 times as wide and at suture approximately as long as pronotum (see ratio EL/PL); humeral angles pronounced; puncturation very fine and dense; interstices with shallow microsculpture (Fig. 60). Hind wings fully developed.

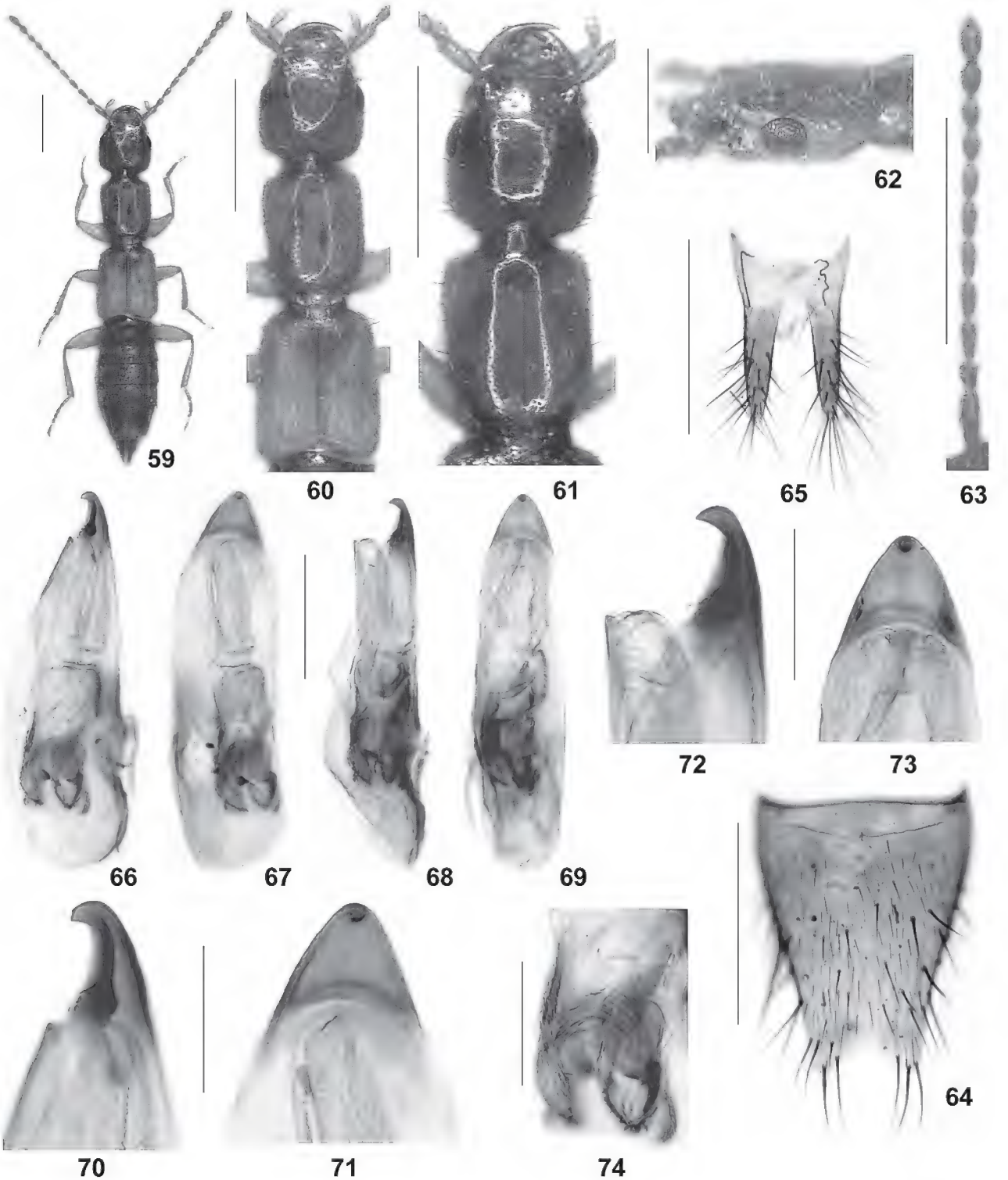
Legs of similar morphology as in *M. testaceus*; metatarsomere I approximately as long as the combined length of II+III.

Abdomen approximately as wide as elytra or slightly narrower, widest at segment VI; puncturation very fine and dense; posterior margin of tergite VII with palisade fringe.

♂: posterior excision of sternite VIII moderately deep, less so than in *M. testaceus* (Fig. 64); segments IX and X similar to those of *M. testaceus*, valvulae of segment IX more than twice as long as tergite X (Fig. 65); aedeagus of similar general morphology as in *M. testaceus*, but smaller (see measurements), less slender, apically distinctly broader, shorter, and more strongly sclerotised (Figs. 66–74).

Intraspecific variation

Maximum/minimum ratios: AL: 1.11; EyL: 1.07; POL: 1.14; HL: 1.07; HW: 1.08; PW: 1.11; PL: 1.12; EL: 1.20; TiL: 1.07; TaL: 1.07; ML: 1.00; TL: 1.19; EyL/POL: 1.18; HL/HW: 1.03; PW/HW: 1.03; PL/PW: 1.06; EL/PL: 1.09; TiL/TaL: 1.05.



Figs. 59–74. *Micrillus irakensis* (Cameron) from Israel (59–60, 62–67, 70–71, 74) and from Irak (61: holotype; 68–69, 72–73). – **59**. Habitus. **60**. Forebody. **61**. Head and pronotum. **62**. Head in lateral view. **63**. Antenna. **64**. Male sternite VIII. **65**. Male abdominal segments IX–X. **66–69**. Aedeagus in lateral and ventral view. **70–73**. Apex of aedeagus in lateral and ventral view. **74**. Internal structures of aedeagus. – Scale bars: 1.0 mm (59–61, 63), 0.5 mm (62, 64–65), 0.2 mm (66–69), 0.1 mm (70–74).

In the few specimens available, intraspecific variation was low in comparison to other species of the genus.

Comparative notes

The species is readily distinguished from all other species of the *M. testaceus* group especially by the concave posterior margin of the head and by the male sexual characters.

Distribution and bionomics

The species was previously known from the surroundings of Baghdad, Iraq. It is here recorded from Israel for the first time (Fig. 58). The material with labels indicating dates was collected during the period from June through August. One of the specimens from Israel was taken at a light source.

3.2.5 *Micrillus hypogaeus* (Peyerimhoff, 1907) (Figs. 47, 75–85)

Scymbalium hypogaeum Peyerimhoff, 1907: 248 f.

Type material examined

Lectotype ♂, here designated: "Bou Zagza [sic] Algérie, 10.IV.07 / Lectotypus H. Coiffait 1970 / *Micrillus hypogaeus* Peyer / Lectotypus ♂ *Scymbalium hypogaeum* Peyerimhoff desig. V. Assing 2007 / *Micrillus hypogaeus* (Peyerimhoff) det. V. Assing 2007" (MNHNP). – Paralectotypes: 2 ♀♀: "Bou Zegza, 11.V.1907 / *hypogaeum* types" (MNHNP); 1 ♂: "dj. Bou Zegza pr. Alger / *Scymbalium hypogaeum* m. / Cotypus *Scimbalium hypogaeum* Peyerimhoff" (NHMW); 1 ♀: Djebel Bou Zegza 4 / *subterraneum* Raffr. var. / *Scimbalium hypogaeum* m. typ. / R. I. Sc. N. B. 17479 Coll. et det. A. Fauvel (IRSNB).

Additional material examined
(total, including types: 7 exs.)

Algeria: 2 exs., Djebel Bou Zegza (NHMW, cAss).

Comments

The original description is based on an unspecified number of syntypes found "au djebel bou-Zegza" near the grotte Rhar-Ifri (Peyerimhoff 1907). Three syntypes, a male and two females, were found in the Peyerimhoff collection at the MNHNP and two syntypes, a male and a female, were located in the collections of the NHMW and the IRSNB, respectively. The male from the Peyerimhoff collection was labelled as the lectotype by Coiffait, but the designation was never published. It is here designated as the lectotype.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 6): AL: 2.17–2.50, 2.29; EyL: 0.05; POL: 0.53–0.63, 0.58; HL: 0.90–1.06, 0.97; HW: 0.88–1.03, 0.93; PW: 0.82–0.92, 0.87; PL: 0.91–1.02, 0.96; EL: 0.57–0.62, 0.61; TiL: 0.89–1.04, 0.98; TaL: 0.82–0.91, 0.87; ML: 0.76–0.79, 0.77; TL: 5.3–5.8, 5.5; EyL/POL: 0.08–0.10, 0.09; HL/HW: 1.03–1.08, 1.04; PW/HW: 0.90–0.97, 0.93; PL/PW: 1.10–1.13, 1.11; EL/PL: 0.61–0.66, 0.63; TiL/TaL: 1.09–1.15, 1.13.

Habitus as in Fig. 75. Coloration of body including appendages usually uniformly reddish, with tarsomeres V pale yellowish.

Head of similar shape as in *M. scabrosus*; puncturation coarse, approximately as coarse as in *M. scabrosus*, moderately dense in lateral dorsal areas and sparse in median dorsal area; interstices in lateral dorsal area on average 1.5–2 times as wide as diameter of punctures (Fig. 76); microsculpture present, but very shallow. Eye rudiments minute, without ommatidia (Fig. 77). Antenna and maxillary palpus similar to those of *M. scabrosus*, but the former on average slightly shorter (Fig. 78).

Pronotum of similar relative size as in *M. scabrosus*, but somewhat more distinctly tapering posteriad (Fig. 76); puncturation as in *M. scabrosus*; microsculpture absent.

Elytra very short (see ratio EL/PL and Fig. 76); humeral angles almost obsolete; surface depressed, laterally usually with shallow oblong impression on either side; puncturation dense, but ill-defined and shallow; microsculpture absent. Hind wings completely reduced.

Metatarsomere I somewhat longer than II, but shorter than the combined length of II+III.

Abdomen approximately 1.3 times as wide as elytra; maximal width at segment V; puncturation somewhat rugose, resembling that of *M. scabrosus* (Fig. 79); microsculpture shallow; posterior margin of tergite VII without palisade fringe.

♂: sternite VII unmodified; posterior margin of sternite VIII shallowly triangularly excised (Fig. 80); segments IX and X on the whole similar to those of *M. scabrosus*, but valvulae of segment IX shorter; aedeagus with apex of ventral process bifid and strongly bent dorsad (Figs. 81–85).

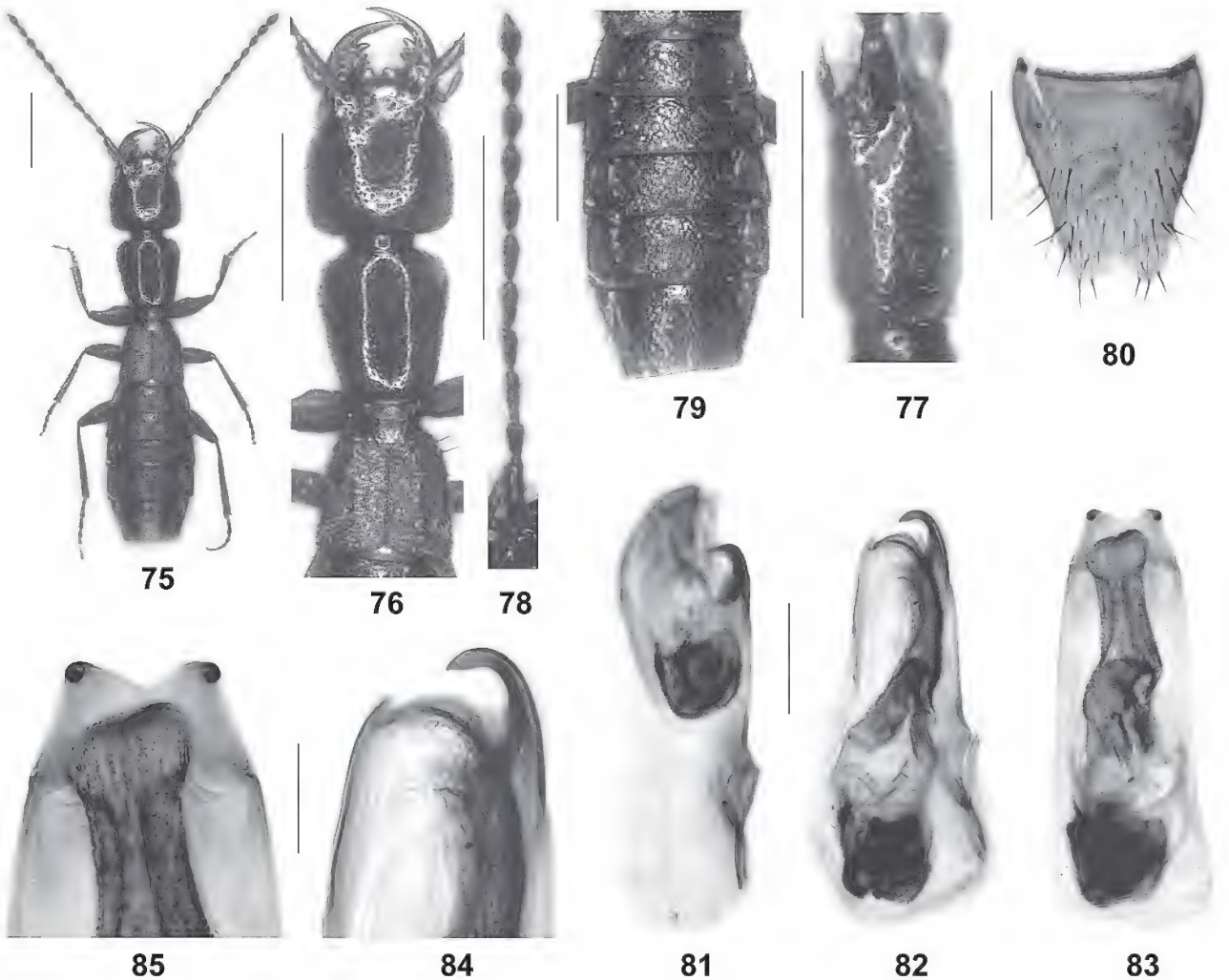
Intraspecific variation

Maximum/minimum ratios: AL: 1.15; EyL: 1.17; POL: 1.20; HL: 1.18; HW: 1.17; PW: 1.13; PL: 1.13; EL: 1.08; TiL: 1.17; TaL: 1.11; ML: 1.04; TL: 1.09; EyL/POL: 1.33; HL/HW: 1.05; PW/HW: 1.08; PL/PW: 1.03; EL/PL: 1.09; TiL/TaL: 1.05.

In the few specimens available, intraspecific variation was comparatively low.

Comparative notes

From the similar *M. scabrosus*, *M. hypogaeus* is readily distinguished by the much smaller eye rudiments, the much shorter elytra, and various other characters (see description above). It is separated from all its congeners by the distinctive morphology of the aedeagus, from most species also by the strongly reduced eyes, the short elytra,



Figs. 75–85. *Micrillus hypogaeus* (Peyerimhoff). – **75**. Habitus. **76**. Forebody. **77**. Head in lateral view. **78**. Antenna. **79**. Abdominal segments III–VII. **80**. Male sternite VIII. **81–83**. Aedeagus in lateral and ventral view. **84–85**. Apex of aedeagus in lateral and ventral view. – Scale bars: 1.0 mm (75–79), 0.5 mm (80), 0.2 mm (81–83), 0.1 mm (84–85).

and the absence of a palisade fringe at the posterior margin of tergite VII. For characters separating it from *M. subterraneus* and *M. tenuipennis*, which have similarly small eye rudiments and short elytra, see the comparative notes in the following sections.

Distribution and bionomics

The species has become known only from the type locality and its vicinity near Algier (Fig. 47). The type specimens were discovered under large stones at an altitude of approximately 800 m in April and May (Peyerimhoff 1907).

3.2.6 *Micrillus subterraneus* Raffray, 1873 (Figs. 47, 86–96)

Micrillus subterraneus Raffray, 1873: 362 f.

Type material examined

Syntype ♀: "Raffray / Coll. P. Boppe, Le Moult vendit / Syntypus ♀ *Micrillus subterraneus* Raffray rev. V. Assing 2007" (IRSNB).

Additional material examined
(total, including type: 44 exs.)

Algeria: 7 exs., Mouzaïa (DEI, HNHM, NHMW, cAss); 4 exs., Mouzaïa-Mines (NHMW, SMTD); 8 exs., Massif de Mouzaïa (BMNH, IRSNB, NHMW); 7 exs., Zaoria de Mouzaïa (HNHM, cAss, cTro); 3 exs., Mouzaïa, Dritka [Dvitka?], leg. Peyerimhoff (NHMW); 1 ex., Mouzaïa (IRSNB); 3 exs., Algier (SMF); 1 ex., Blida (SMF); 1 ♀, Algier, Mizrana, M. Tizzirt (MCSNM); 1 ♀, Medeah (IRSNB); 1 ♀, Medeah env., Mt. Nador (IRSNB); 1 ♀, Medeah, leg. Sicard (BMNH); 1 ♀, Djebel Ouarsenis [35°53'N, 1°37'E] (IRSNB).

Locality not indicated: 4 exs. (IRSNB).

Comments

The original description is based on an unspecified

number of syntypes from the "environs d'Alger" (RAFFRAY 1873). Only one type specimen was found in the collections of the IRSNB. Since it is a female and there is at least some hope that a male may eventually be located, it is not designated as the lectotype.

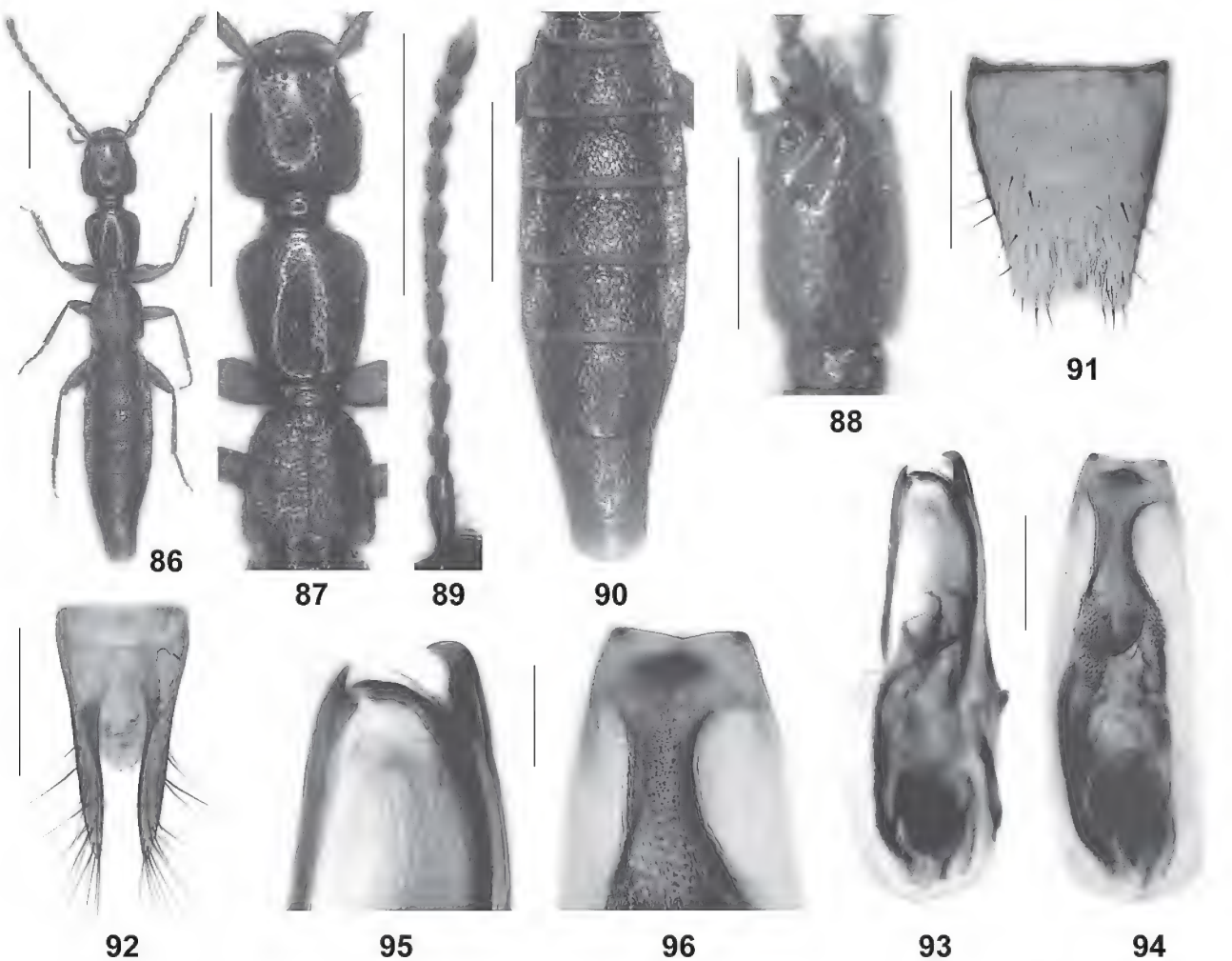
Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 14): AL: 1.68–2.01, 1.91; EyL: 0.03–0.05, 0.04; POL: 0.41–0.45, 0.43; HL: 0.71–0.79, 0.75; HW: 0.71–0.79, 0.76; PW: 0.71–0.79, 0.76; PL: 0.82–0.92, 0.87; EL: 0.53–0.57, 0.55; TiL: 0.77–0.85, 0.81; TaL: 0.66–0.74, 0.70; ML: 0.79–0.80, 0.79; TL: 4.2–5.9, 4.7; EyL/POL: 0.07–0.13, 0.10; HL/HW: 0.97–1.02, 0.99; PW/HW: 0.97–1.02, 1.00; PL/PW: 1.12–1.17, 1.15; EL/PL: 0.59–0.65, 0.63; TiL/TaL: 1.10–1.20, 1.15.

Habitus as in Fig. 86. Coloration of body including appendages usually uniformly reddish, with tarsomeres V pale yellowish.

Head approximately as wide as long or weakly transverse, of similar shape as in *M. scabrosus* and *M. hypogaeus*, but on average smaller in relation to pronotum, approximately as wide as or slightly narrower than pronotum (see ratio PW/HW and Fig. 87); puncturation on average coarser and denser than in *M. hypogaeus*, interstices in lateral dorsal area on average approximately as wide as diameter of punctures or only slightly wider; surface with distinct microsculpture and subdued shine. Eye rudiments minute, without ommatidia (Fig. 88). Antenna slightly shorter and less slender than in *M. hypogaeus* (Fig. 89). Maxillary palpus similar to that of *M. scabrosus*.

Pronotum of similar shape and puncturation as in *M. hypogaeus* (Fig. 87); microsculpture absent.



Figs. 86–96. *Micrillus subterraneus* Raffray. – **86**. Habitus. **87**. Forebody. **88**. Head in lateral view. **89**. Antenna. **90**. Abdominal segments III–VIII. **91**. Male sternite VIII. **92**. Male abdominal segments IX–X. **93–94**. Aedeagus in lateral and ventral view. **95–96**. Apex of aedeagus in lateral and ventral view. – Scale bars: 1.0 mm (86–87, 89–90), 0.5 mm (88, 91–92), 0.2 mm (93–94), 0.1 mm (95–96).

Elytra very short (see ratio EL/PL and Fig. 87); humeral angles almost obsolete; surface depressed, laterally with or without shallow oblong impression on either side; puncturation dense, irregular, and ill-defined; microsculpture absent. Hind wings completely reduced.

Metatarsomere I approximately as long as the combined length of II+III.

Abdomen approximately 1.20–1.25 times as wide as elytra; maximal width at segment V; puncturation somewhat rugose to granulose, similar to that of *M. scabrosus*, but usually denser (Fig. 90); microsculpture distinct; posterior margin of tergite VII without palisade fringe.

♂: sternite VII unmodified; posterior margin of sternite VIII shallowly triangularly excised (Fig. 91); segments IX and X on the whole similar to those of *M. scabrosus*, but valvulae of segment IX shorter, approximately twice as long as tergite X (Fig. 92); general morphology of aedeagus similar to that of *M. hypogaeus*, but apex less distinctly bifid and less strongly bent dorsad (Figs. 93–96).

Intraspecific variation

Maximum/minimum ratios: AL: 1.20; EyL: 1.75; POL: 1.11; HL: 1.11; HW: 1.11; PW: 1.12; PL: 1.13; EL: 1.09; TiL: 1.10; TaL: 1.11; ML: 1.02; TL: 1.40; EyL/POL: 1.75; HL/HW: 1.05; PW/HW: 1.05; PL/PW: 1.05; EL/PL: 1.11; TiL/TaL: 1.09.

As is shown by the above ratios, intraspecific variation is about as low as that of *M. hypogaeus*.

Comparative notes

From *M. hypogaeus*, the only other microphthalmous congener from Algeria, *M. subterraneus* is readily distinguished by smaller size (little or no overlap, see measurements), a less oblong and smaller head (in relation to pronotum), shorter antennae, a more oblong pronotum (little overlap), coarser and denser puncturation of the head, more pronounced microsculpture of the head, a longer metatarsomere I, and by the morphology of the aedeagus. For additional characters see the redescription above.

Distribution and bionomics

The species has become known only from the type locality and its vicinity near Algier (Fig. 47). The type specimens were discovered under large stones on clay soil in December (Raffray 1873).

3.2.7 *Micrillus tenuipennis* **n. sp.** (Figs. 47, 97–103)

Type material

Holotype ♂: "Morocco (Taza) [08], ca. 30 km SE Tissa, 34°14'N, 4°27'W, field margins, loam, clay, under stones, 25.II.2004, leg. D. W. Wrase / Holotypus ♂ *Micrillus tenuipennis* sp. n. det. V. Assing 2007" (cAss).

Paratype ♀: "Morocco – 30 km NW Taza, Sebt-des-Beni-Frassen, 34°20N, 04°22W, fallow land, 22.II.2004, leg. Assmann" (cSch).

Etymology

The name (Lat., adj.: with narrow wings) refers to the conspicuously slender elytra, a character separating the new species from all other *Micrillus* species.

Description

Measurements (in mm) and ratios (holotype, paratype): AL: 2.56, 2.32; EyL: 0.06, 0.07; POL: 0.51, 0.47; HL: 0.94, 0.85; HW: 0.93, 0.82; PW: 0.84, 0.76; PL: 0.99, 0.89; EL: 0.65, 0.63; TiL: 0.97, 0.86; TaL: 0.82, 0.76; ML: 0.83, – ; TL: 6.0, 5.4; EyL/POL: 0.12, 0.15; HL/HW: 1.01, 1.05; PW/HW: 0.90, 0.93; PL/PW: 1.18, 1.18; EL/PL: 0.67, 0.71; TiL/TaL: 1.19, 1.14.

Habitus as in Fig. 97. Coloration of body uniformly pale to dark reddish; legs dark yellowish to yellowish brown, with tarsomeres V pale yellowish.

Head with shape, puncturation, microsculpture, antennae, and maxillary palpi as in *M. scabrosus* (Fig. 98). Eyes reduced to minute rudiments, without ommatidia (Fig. 99).

Pronotum of similar shape and puncturation as in *M. scabrosus*; microsculpture absent (Fig. 98).

Elytra very short (see ratio EL/PL and Fig. 98) and slender, in both type specimens approximately 0.95 times as wide as pronotum; humeral angles almost obsolete; surface depressed, laterally with shallow oblong impression on either side; puncturation dense, irregular, and rather ill-defined; microsculpture absent. Hind wings completely reduced.

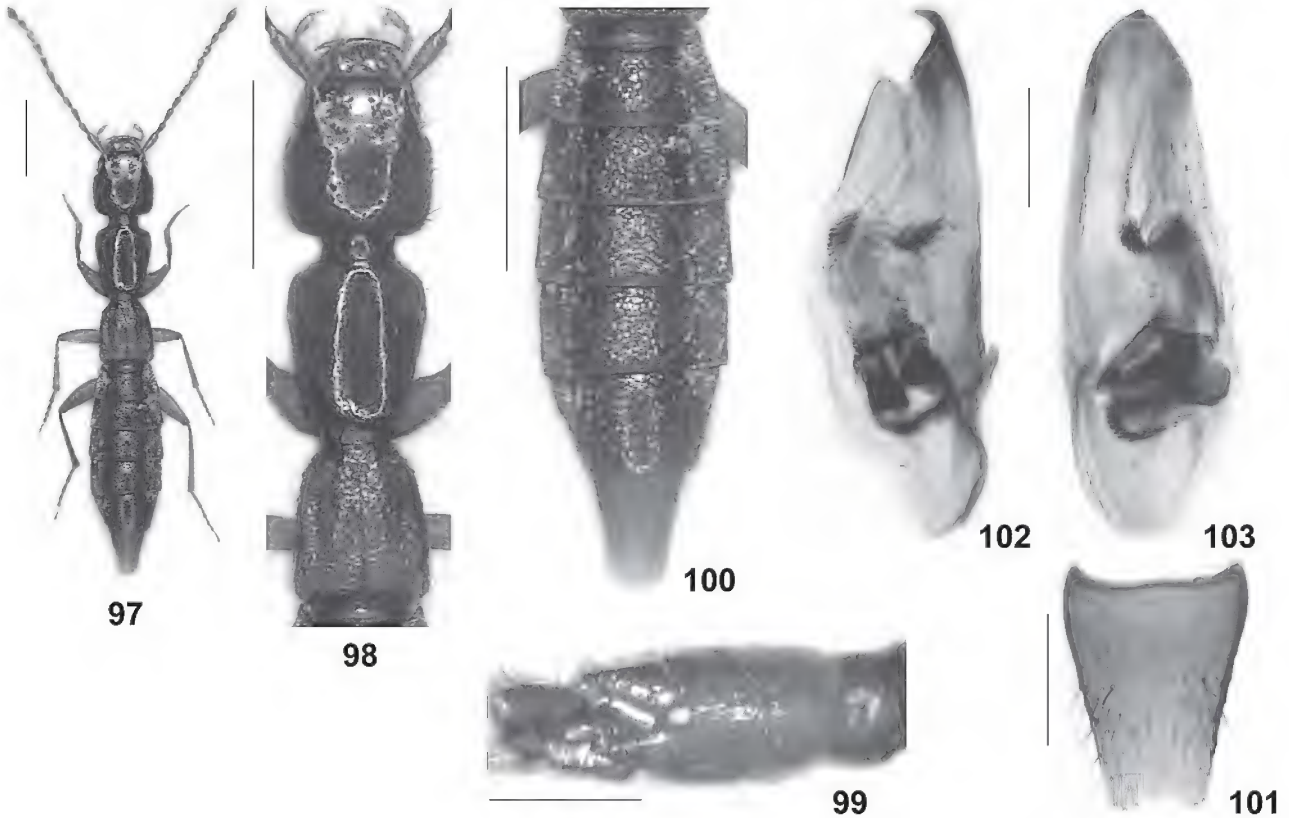
Metatarsomere I approximately as long as the combined length of II+III.

Abdomen approximately 1.3 times as wide as elytra; maximal width at segments V–VI; puncturation rather coarse, somewhat irregular, and weakly delimited (Fig. 100); microsculpture shallow; posterior margin of tergite VII without palisade fringe.

♂: sternite VII unmodified; posterior margin of sternite VIII concavely excised (Fig. 101); segments IX and X on the whole similar to those of *M. scabrosus*, valvulae of segment IX slightly more than twice as long as tergite X; aedeagus in ventral view apically pointed, in lateral view slightly bent dorsad (Figs. 102–103).

Intraspecific variation

Maximum/minimum ratios: AL: 1.11; EyL: 1.13; POL: 1.10; HL: 1.10; HW: 1.11; PW: 1.12; PL: 1.11; EL: 1.02; TiL: 1.12; TaL: 1.08; ML: 1.02; TL: 1.11; EyL/POL: 1.23; HL/HW: 1.04; PW/HW: 1.03; PL/PW: 1.00; EL/PL: 1.08; TiL/TaL: 1.04.



Figs. 97–103. *Micrillus tenuipennis* n. sp. – **97**. Habitus. **98**. Forebody. **99**. Head in lateral view. **100**. Abdominal segments III–VIII. **101**. Male sternite VIII. **102–103**. Aedeagus in lateral and ventral view. – Scale bars: 1.0 mm (97–98, 100), 0.5 mm (99, 101), 0.2 mm (102–103).

The holotype is somewhat larger than the paratype (see measurements), but this variation is within the usual range of other microphthalmous species from North Africa.

Comparative notes

From all its congeners, *M. tenuipennis* is distinguished by the male primary and secondary sexual characters. The only other *Micrillus* species known from Morocco are *M. testaceus* and *M. scabrosus*, both of which have distinctly larger eyes composed of ommatidia and broader elytra (elytra wider than pronotum). From the Algerian *M. hypogaeus* and *M. subterraneus*, which, too, have minute eye rudiments without ommatidia, *M. tenuipennis* is additionally separated by larger eye rudiments and by more slender elytra (in *M. hypogaeus* and *M. subterraneus* approximately as wide as pronotum).

Distribution and bionomics

The type specimens were collected in two localities in the surroundings of Taza, northern Morocco (Fig. 47). They were found under stones on arable land and fallows in February.

3.2.8 *Micrillus biskrensis* (Fauvel, 1898) (Figs. 47, 104–110)

Scymbalium biskrense Fauvel, 1898: 98.

Type material examined

Lectotype ♀, here designated: "Biskra, Algérie / *biskrense* Fvl. / R. I. Sc. N. B. Coll. et det. A. Fauvel / Ex-Typis / Lectotypus ♀ *Scymbalium biskrense* Fauvel desig. V. Assing 2007 / *Micrillus biskrensis* (Fauvel) det. V. Assing 2007" (IRSNB).

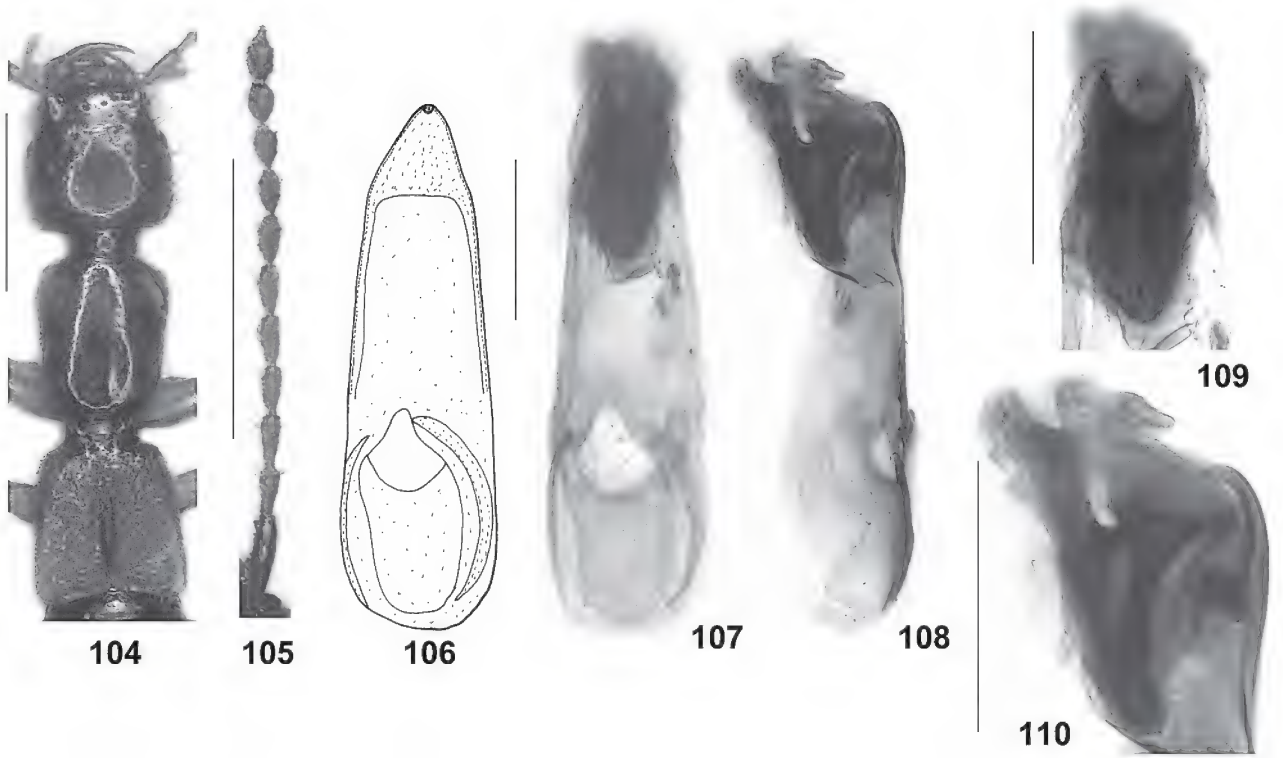
Additional material examined (total, including type: 3 exs.)

Algeria: 1 ex., Biskra (IRSNB); 1 ex., Biskra, 9.V.1886 (MNHNP).

Comments

In the original description of *Scymbalium biskrense*, Fauvel (1898) states that he did not see a male. Since he does not state the number of females, the specimen from Biskra in his collection has syntype status. It is here designated as the lectotype.

The non-type male, on which the diagnosis of this species is primarily based, is somewhat larger than the lecto-



Figs. 104–110. *Micrillus biskrensis* (Fauvel). – **104**. Forebody. **105**. Antenna. **106**. Outline of aedeagus in ventral view. **107–108**. Aedeagus in ventral and lateral view. **109**. Internal structures of aedeagus in ventral view. **110**. Apex of aedeagus in lateral view. – Scale bars: 1.0 mm (104–105), 0.2 mm (106–110).

type and has completely reduced hind wings, whereas the lectotype is macropterous. More material is needed to confirm that they are indeed conspecific. The lectotype is practically indistinguishable from small pale macropterous specimens of *M. testaceus*, which have been seen from Israel, for instance.

The illustrations of the aedeagus provided by Coiffait (1980, 1982) – figures 3G–H and 52G–H, respectively – are highly misleading. An examination of the male on which these illustrations are based revealed that what he figures as the ventral process in fact refers to the – somewhat extruded – internal structures.

Redescription

Measurements (in mm) and ratios (lectotype, non-type male): AL: 1.74, 2.07; EyL: 0.13, 0.14; POL: 0.34, 0.41; HL: 0.71, 0.84; HW: 0.69, 0.85; PW: 0.67, 0.79; PL: 0.80, 0.92; EL: 0.68, 0.70; TiL: 0.68, 0.77; TaL: 0.54, – ; ML: – , 0.66; TL: 4.7, 5.6; EyL/POL: 0.38, 0.33; HL/HW: 1.02, 0.99; PW/HW: 0.97, 0.93; PL/PW: 1.19, 1.17; EL/PL: 0.85, 0.76; TiL/TaL: 1.25, – .

Coloration of body uniformly yellowish brown to reddish brown, with the appendages slightly paler.

Head approximately as wide as long, of similar shape as in *M. testaceus* (Fig. 104); puncturation and microsculpture as in *M. testaceus*. Eyes of similar size as in *M. testaceus*. Antenna (Fig. 105) as in small specimens of *M. testaceus*. Maxillary palpus with palpomeres III and IV slightly shorter and less slender than in *M. testaceus*.

Pronotum of similar shape and puncturation as in *M. testaceus* (Fig. 104); microsculpture absent.

Elytra of variable length (see ratio EL/PL); puncturation dense and ill-defined; microsculpture absent or very shallow. Hind wings completely reduced or present.

Metatarsomere I approximately as long as the combined length of II+III or slightly shorter.

Abdomen 1.10–1.18 times as wide as elytra; maximal width at segments V–VI; puncturation fine, less dense than in *M. testaceus*; microsculpture shallow; posterior margin of tergite VII with palisade fringe.

♂: sternite VII unmodified; posterior margin of sternite VIII with moderately deep triangular excision; segments IX and X as in *M. testaceus*; general morphology of aedeagus similar to that of *M. scabrosus* (Figs. 106–110).

Intraspecific variation

The lectotype and the non-type male considerably differ in size. Also, the male has completely reduced hind wings, relatively short and depressed elytra, and relatively smaller eyes, whereas the lectotype has (fully?) developed

hind wings, relatively longer and – in cross-section – slightly convex elytra, and relatively larger and more bulging eyes.

Comparative notes

From pale coloured specimens of *M. testaceus*, *M. biskrensis* is reliably distinguished only by the smaller, broader, and apically more distinctly sclerotised aedeagus, as well as by the shape of the internal structures of the aedeagus. From *M. scabrosus*, it is separated by smaller body size, finer puncturation of the elytra and the abdomen, the deeper posterior excision of the male sternite VIII, and by the shape of the internal structures of the aedeagus. From the two microphthalmous species occurring in Algeria, *M. hypogaeus* and *M. subterraneus*, it conspicuously differs by the distinctly larger eyes with ommatidia, the longer and broader elytra, the presence of a palisade fringe at the posterior margin of the abdominal tergite VII, as well as by the shape of the aedeagus.

Distribution and bionomics

Micrillus biskrensis has become known only from the surroundings of Biskra (Fig. 47). Bionomic data are not available.

3.2.9 *Micrillus aegyptiacus* (Bernhauer, 1910) (Figs. 111–126)

Scymbalium aegyptiacum Bernhauer, 1910: 256.
Scymbalium (Schatzmayria) bernhaueri Koch, 1934: 87 ff.; **n. syn.**

Type material examined

Scymbalium aegyptiacum: Holotype ♀ [somewhat damaged, without antennae, head and pronotum separated from remainder of body]: "Aegypten Boehm / *aegyptiacum* Brh. Typus / Chicago NHMus, M. Bernhauer Collection / Holotypus ♀ *Scymbalium aegyptiacum* Bernhauer rev. V. Assing 2007 / *Micrillus aegyptiacus* (Bernhauer) det. V. Assing 2007" (FMNH).

Scymbalium bernhaueri: Lectotype ♂, here designated: "Barrage Eg., 10.IX.1933, W. Wittmer / Cotypus / Lectotypus ♂ *Scymbalium bernhaueri* Koch desig. V. Assing 2007 / *Micrillus aegyptiacus* (Bernhauer) det. V. Assing 2007" (MCSNM). – Paralectotypes: 23 exs.: same data as lectotype (MCSNM); 2 exs.: same labels as lectotype, but "Typus" (MCSNM); 1 ex.: "Barrage Eg., 10.IX.1933, W. Wittmer / Cotypus / Coll. Museo ent. 'Pietro Rossi' Duino / *Scymbalium Bernhaueri* nov. spec. i. litt. det. C. Koch / Syntypus *Scymbalium bernhaueri* Koch, 1934, labelled by MNHUB 2006" (MNHUB); 1 ex.: "Barrage Eg., 10.IX.1933, W. Wittmer / Cotype / Cotypus / Coll. Museo ent. 'Pietro Rossi' Duino / Egypt B. M. 1934-135." (BMNH); 1 ex.: "Eg. Cairo, Pyramidi, 2.X.1933, W. Wittmer / Typus" (MCSNM); 4 exs.: same labels, but "Cotypus" (MCSNM).

Additional material examined
(total, including types: 52 exs.)

Egypt: 3 exs., Barrage, 10.IX.1933, leg. Wittmer (NHMW); 1 ex., Barrage, 21.IX.1933, leg. Wittmer (BMNH); 3 exs., Cairo, leg. Schatzmayr & Koch (NHMW, cAss); 1 ex., "Barrage Eg., 12.IX.33, W Wittmer / Coll. Museo ent. 'Pietro Rossi' Duino / Cotypus / Emmerich Reitter vend. III.1943 / Cotypus *Scimbalium Bernhaueri* C. Koch / ex coll. Scheerpeltz" (NHMW); 6 exs., "Barrage Eg., 12.IX.33, W Wittmer / Coll. Museo ent. 'Pietro Rossi' Duino / Cotypus" (SMF); 2 exs., "Barrage Eg., 12.IX.33, W Wittmer / Coll. Museo ent. 'Pietro Rossi' Duino / Cotypus" (BMNH); 1 ex., Barrage, 31.VIII.1933, leg. Wittmer (cTro); 1 ex., Fayoum (IRSNB).

Comments

The original description of *S. aegyptiacum* is explicitly based on a single specimen ("ein einzelnes Exemplar") from "Aegypten" (Bernhauer 1910). According to Koch (1934), *S. bernhaueri* is distinguished from *S. aegyptiacum* by the width of the head in relation to the pronotum, eye size, the shape of the temples, the length and width of the elytra, as well as by the puncturation of the pronotum and the abdomen. A comparison and dissection of the type material of both taxa and an examination of additional material, some of which had evidently been identified as *S. aegyptiacum* or *S. bernhaueri* by Koch himself, revealed that they are all conspecific and that the characters believed by Koch (1934) to be distinguishing characters are all highly variable (see measurements below and Figs. 124–125). Consequently, *Micrillus bernhaueri* is here placed in the synonymy of the senior name *M. aegyptiacus*.

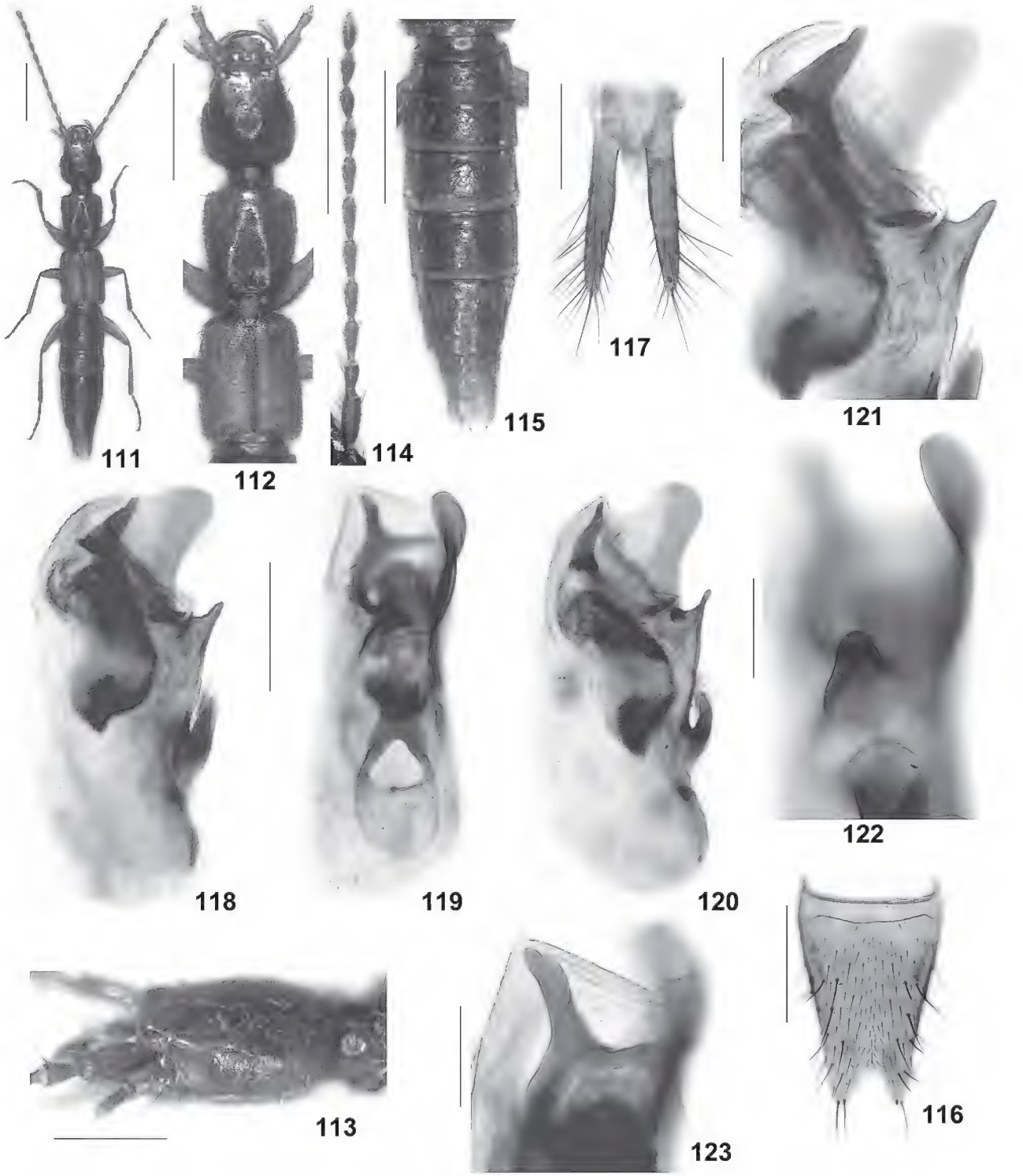
The original description of *Scymbalium bernhaueri* is based on an unspecified number of syntypes collected "am 10.9.1933 bei Barrage bei Cairo in Anzahl und am 2.10.1933 bei den Pyramiden von Ghizeh in wenigen Exemplaren" (Koch 1934). One of the numerous syntypes in the collection of the MCSNM is here designated as the lectotype. Some of the specimens from the NHMW, BMNH, and SMF are labelled as "Cotypus", but their type status must be considered doubtful, since either the localities and dates indicated on the labels, or the identification ("*S. aegyptiacum*") do not match the details given in the original description.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 17): AL: 2.59–3.05, 2.79; EyL: 0.20–0.29, 0.23; POL: 0.33–0.41, 0.38; HL: 0.88–0.94, 0.90; HW: 0.82–0.94, 0.88; PW: 0.82–0.95, 0.86; PL: 0.94–1.09, 1.00; EL: 0.85–1.10, 0.93; TiL: 0.92–0.98, 0.95; TaL: 0.80–0.89, 0.85; ML: 0.63–0.69, 0.66; TL: 5.6–6.6, 5.9; EyL/POL: 0.48–0.86, 0.60; HL/HW: 0.99–1.09, 1.02; PW/HW: 0.94–1.03, 0.97; PL/PW: 1.12–1.20, 1.17; EL/PL: 0.86–1.04, 0.93; TiL/TaL: 1.09–1.17, 1.12.

Habitus as in Fig. 111. Head, pronotum, abdomen, and antennae reddish, occasionally partly and diffusely infuscated; elytra and legs dark yellowish to reddish yellow.

Head approximately as wide as long or weakly oblong (see ratio HL/HW and Fig. 112); puncturation in lateral and in posterior dorsal area moderately coarse and moderately dense, with interstices on average approximately as



Figs. 111–123. *Micrillus aegyptiacus* (Bernhauer). – **111**. Habitus. **112**. Forebody. **113**. Head in lateral view. **114**. Antenna. **115**. Abdominal segments III–VIII. **116**. Male sternite VIII. **117**. Male abdominal segments IX–X. **118–120**. Aedeagus in lateral and ventral view. **121–123**. Apex of aedeagus in lateral and ventral view. – Scale bars: 1.0 mm (111–112, 114–115), 0.5 mm (113, 116–117), 0.2 mm (118–120), 0.1 mm (121–123).

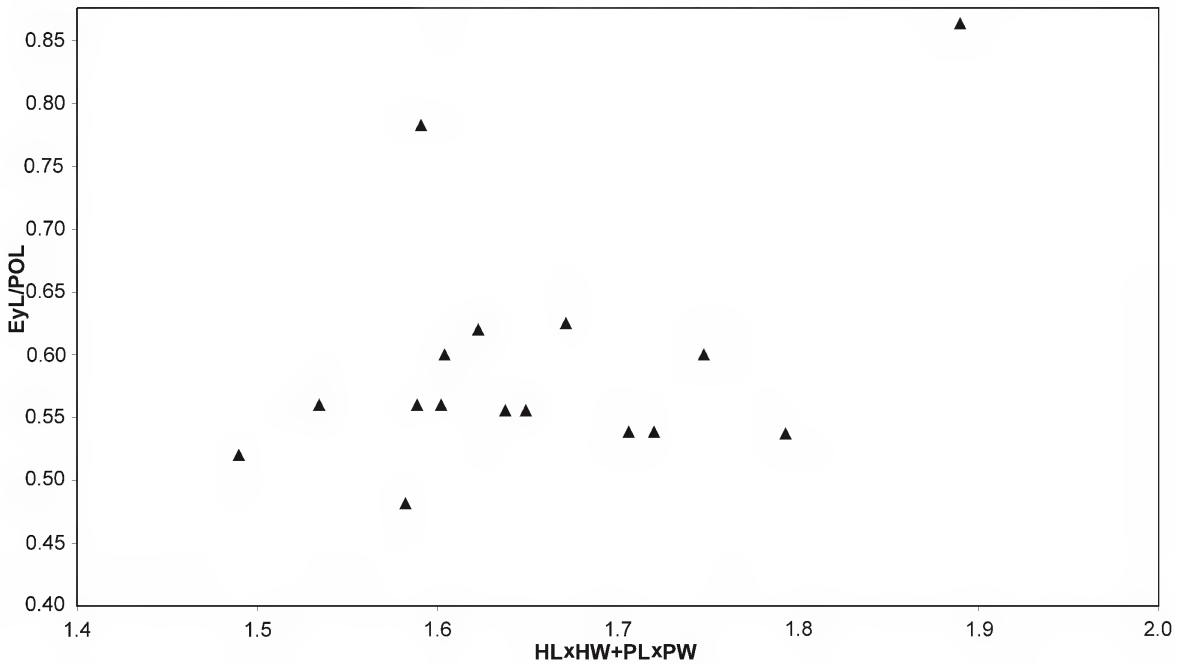


Fig. 124. *Micrillus aegyptiacus* (Bernhauer). Relative eye size (EyL/POL) in relation to body size.

wide as or somewhat wider than diameter of punctures; median dorsal area impunctate or with scattered punctures; microsculpture extremely shallow, in median dorsal area barely noticeable. Eyes relatively large (see ratio EyL/POL and Fig. 113) and distinctly projecting from lateral contours of head in dorsal view. Antenna long and slender (Fig. 114). Maxillary palpus with the terminal joint distinctly shorter than in the species of the *M. testaceus* group, less than half as long as preapical joint, distinctly coniform, and often somewhat flattened.

Pronotum usually narrower than, but occasionally as wide as head, and distinctly oblong (see ratios PW/HW and PL/PW); posterior margin distinctly concave; predominant puncturation extremely fine and rather dense, much finer and denser than in species of the *M. testaceus* group; disc with some scattered interspersed and usually setiferous coarser punctures (Fig. 112).

Elytra relatively long (see ratio EL/PL and Fig. 112), with parallel lateral margins, and with well-developed humeral angles; puncturation fine and very dense; microsculpture very shallow or indistinct. Hind wings fully developed.

Legs slender; metatarsomere I at least slightly longer than the combined length of II+III, but shorter than the combined length of II–IV.

Abdomen approximately as wide as elytra, widest at segments V–VI; tergites with fine puncturation (Fig. 115); posterior margin of tergite VII with palisade fringe.

♂: sternite VII unmodified; posterior margin of sternite VIII deeply triangularly excised (Fig. 116); valvulae of segment IX conspicuously long, more than 3 times as long as tergite X (Fig. 117); aedeagus distinctly asymmetric (Figs. 118–123).

Intraspecific variation

Maximum/minimum ratios: AL: 1.18; EyL: 1.46; POL: 1.23; HL: 1.07; HW: 1.15; PW: 1.17; PL: 1.17; EL: 1.30; TiL: 1.07; TaL: 1.11; ML: 1.10; TL: 1.19; EyL/POL: 1.79; HL/HW: 1.10; PW/HW: 1.10; PL/PW: 1.08; EL/PL: 1.21; TiL/TaL: 1.08.

Relative and absolute eye size and elytral length are subject to considerable intraspecific variation (Figs. 124–125).

Comparative notes

From all its congeners, *M. aegyptiacus* is separated by the highly distinctive shape of the aedeagus. From the species of the *M. testaceus* group, it is additionally distinguished by the very weak microsculpture on the head, the distinctly shorter and more conical terminal joint of the maxillary palpus, the much finer ground puncturation of the pronotum, and by the much longer valvulae of the abdominal segment IX. The only other congener reported from Egypt is *M. torretassoi*, which is readily distinguished from *M. aegyptiacus* by distinctly smaller size alone.

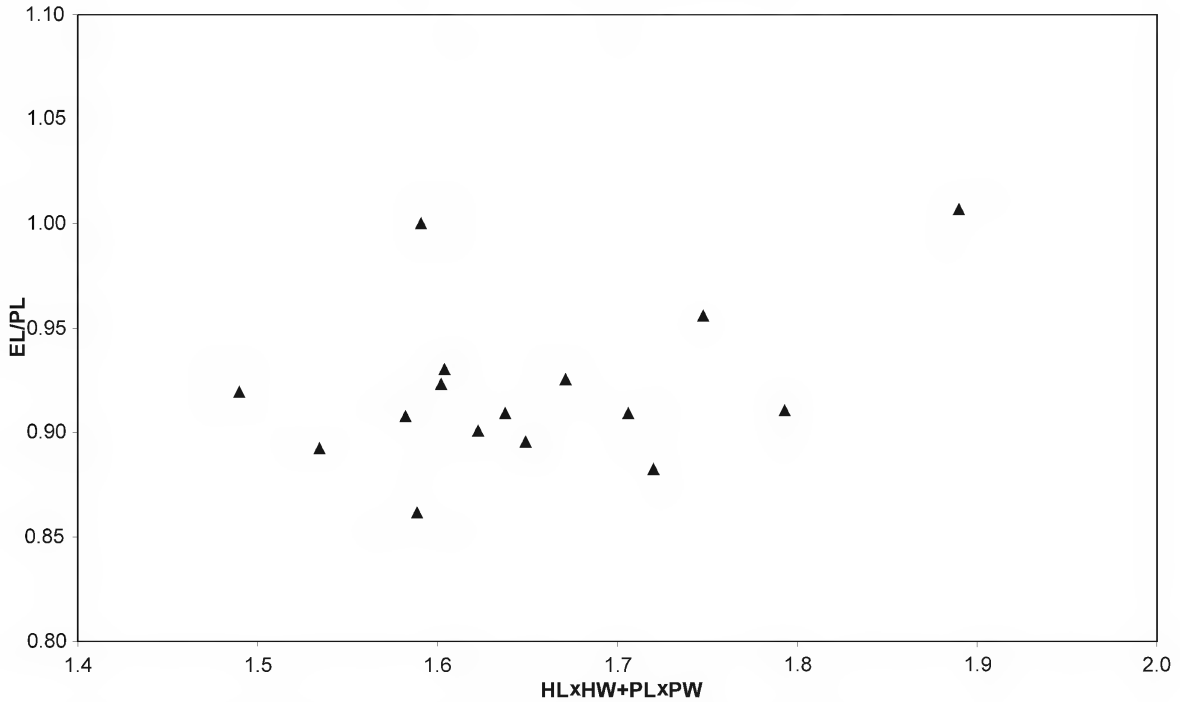


Fig. 125. *Micrillus aegyptiacus* (Bernhauer). Relative elytral length (EL/PL) in relation to body size.

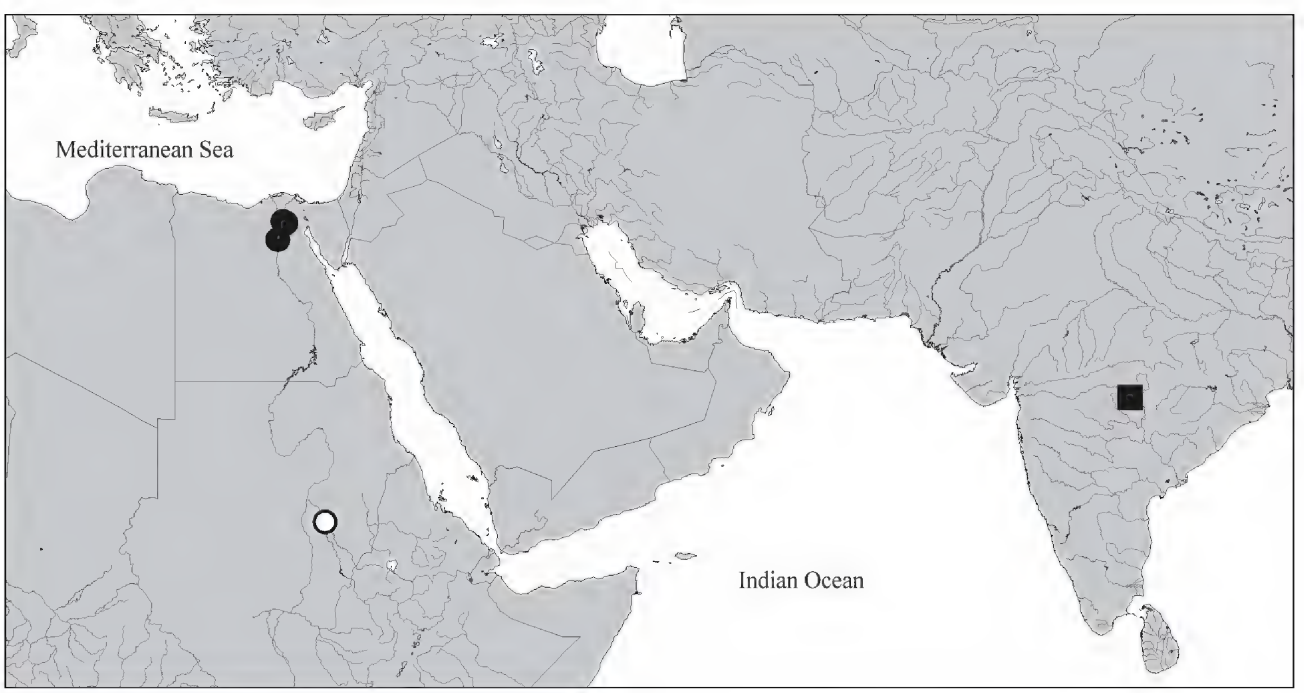


Fig. 126. Distributions of *Micrillus aegyptiacus* (Bernhauer) (●), *M. sudanicus* n. sp. (○), and *M. indicus* (Eppelsheim) (■), based on examined records.

Distribution and bionomics

The species has become known only from some localities near Cairo and from Al Faiyūm in Egypt (Fig. 126). The type specimens of *M. bernhaueri* were found on the bank of the Nile river (Koch 1934). Most of the material examined was collected in September, some specimens also in August and October.

3.2.10 *Micrillus torretassoi* (Koch, 1934) (Figs. 127–143)

Scymbalium (Schatzmayria) torretassoi Koch, 1934: 89 f.
Scymbalium collare Scheerpeltz, 1962: 580 ff.; **n. syn.**

Type material examined

S. torretassoi: Lectotype ♂, here designated: "Kirdassah Eg., 28.IX.1933, W. Wittmer / Typus / Lectotypus ♂ *Scymbalium torretassoi* Koch desig. V. Assing 2007 / *Micrillus torretassoi* (Koch) det. V. Assing 2007" (NHMW). – Paralectotypes: 3 exs.: same labels as lectotype, but "Cotypus" (MCSNM); 11 exs.: "Kirdassah Eg., 28.IX.1933, W. Wittmer" (MCSNM); 1 ex.: "Kirdassah Eg., 28.IX.1933, W. Wittmer / Coll. Museo ent. 'Pietro Rossi' Duino / Cotypus / *Scymbalium Torre-Tassoi* nov. i. litt. det. C. Koch / C. Koch Museo Duino donavit 1934 / Cotypus *Scimbalium Torre-Tassoi* C. Koch / ex coll. Scheerpeltz" (NHMW); 1 ex.: "Kirdassah Eg., 28.IX.1933, W. Wittmer / Cotype / Coll. Museo ent. 'Pietro Rossi' Duino / Cotypus / *Scymbalium Torre-Tassoi* nov. i. litt. det. C. Koch / M. Cameron. Bequest B. M. 1955-147" (BMNH); 1 ex.: "Kirdassah Eg., 28.IX.1933, W. Wittmer / Coll. Museo ent. 'Pietro Rossi' Duino / *Scimbalium Torre Tassoi* Koch" (cTro).

S. collare: Holotype ♀: "Aegypt. Sudan, Bahr el Ghazal b. Bahr el Arab, 4.III.1913 / Bernhauer det. / Holotypus / Dtsch. Entomol. Institut Berlin / ex coll. Scheerpeltz / Typus *Scimbalium collare* O. Scheerpeltz / *Scimbalium collare* m. det. Scheerpeltz 1962 / *Micrillus torretassoi* (Koch) det. V. Assing 2007". – Paratype ♀: "Aegypt. Sudan, Bahr el Ghazal b. Bahr el Arab, 4.III.1913 / Bernhauer det. / Paratypus / Dtsch. Entomol. Institut Berlin / ex coll. Scheerpeltz / Cotypus *Scimbalium collare* O. Scheerpeltz" (NHMW).

Additional material examined (total, including types: 56 exs.)

Egypt: 28 exs. [brachypterous], Cairo, Pyramidi, 2.X.1933, leg. Wittmer (BMNH, IRSNB, MCSNM, MNHUB, NHMW, SMF, SMNS, cAss, cTro); 1 ex. [brachypterous], Cairo, Pyramidi, leg. Koch & Schatzmayr (NHMW); 1 ex., "Pyramides", 8.X.1933, leg. Rabinovitch (HNHM).

Sudan: 1 ex. [macropterous], Wad Medani, Blue Nile, light, 18.X.1979, leg. Königsmann (MNHUB); 1 ex. [macropterous], same data, but 24.X.1979, leg. Hieke (MNHUB); 1 ex. [macropterous], same data, but 23.X.1979, leg. Hieke (MNHUB); 1 ex. [macropterous], same data, but 15.X.1979, leg. Hieke (MNHUB); 2 exs. [macropterous], same data, but 20.X.1979, leg. Hieke (MNHUB, cAss).

Comments

The original description of *S. torretassoi* is based on an unspecified number of syntypes from "Kirdassah, 28.9.1933" (Koch 1934). Numerous syntypes matching these data were found in the collections of the MCSNM, the NHMW and the BMNH. The male syntype from the MCSNM labelled as "Typus" is here designated as the lectotype. Some additional specimens deposited in the NHMW and BMNH, too, are labelled as types and apparently a gift from the collection of the Museum in Duino, but cannot be attributed type status, since they were not collected in the locality indicated in the original description.

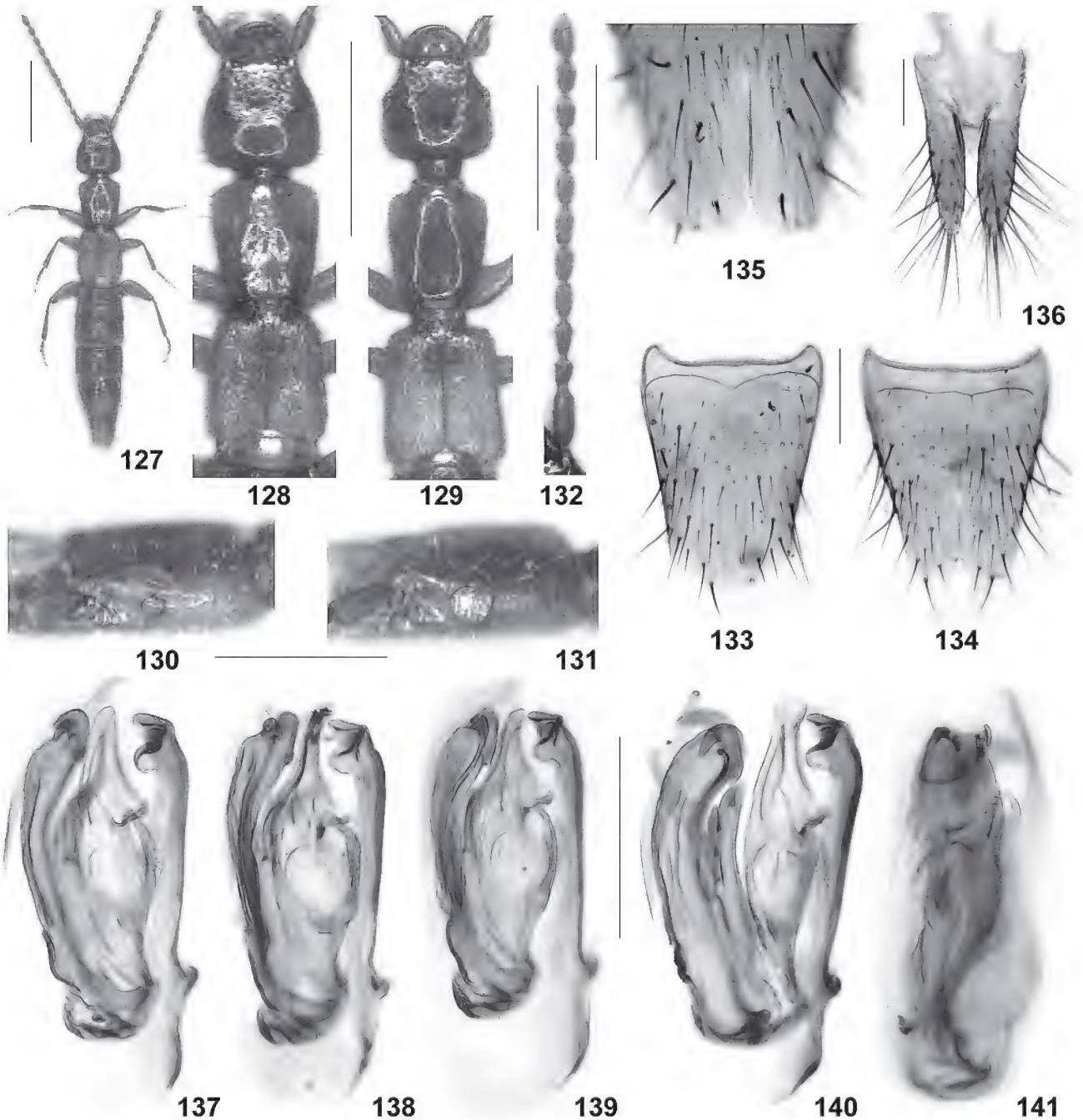
The original description of *S. collare* is based on the holotype and a paratype, both females, from "Ägypt. Sudan, Bahr el Ghazahl [sic]", which is in southern Sudan today. The macropterous and relatively large-eyed type specimens are externally identical to the non-type material from Wad Medani, Sudan (see material examined), whose aedeagus and secondary sexual characters are identical to those of the brachypterous and small-eyed types of *S. torretassoi* and the additional material seen from Egypt. These observations suggest that the species is dimorphic regarding eye size, length of the elytra, and length of the hind wings, and that the types of *S. torretassoi* and *S. collare* are conspecific, so that *S. collare* is a junior synonym of *S. torretassoi*.

Redescription

Measurements (in mm) and ratios (range, arithmetic mean; n = 24): AL: 1.22–1.62, 1.49; EyL (brachypterous morph): 0.06–0.08, 0.07; EyL (macropterous morph): 0.11–0.15, 0.13; POL (brachypterous morph): 0.25–0.30, 0.27; POL (macropterous morph): 0.23–0.26, 0.25; HL: 0.50–0.56, 0.52; HW: 0.53–0.58, 0.55; PW: 0.48–0.54, 0.51; PL: 0.55–0.62, 0.58; EL (brachypterous morph): 0.44–0.48, 0.47; EL (macropterous morph): 0.50–0.63, 0.55; TiL: 0.45–0.54, 0.47; TaL: 0.36–0.45, 0.40; ML: 0.35–0.38, 0.36; TL: 3.1–3.7, 3.4; EyL/POL (brachypterous morph): 0.22–0.29, 0.26; EyL/POL (macropterous morph): 0.41–0.59, 0.51; HL/HW: 0.88–1.04, 0.94; PW/HW: 0.88–0.99, 0.94; PL/PW: 1.10–1.16, 1.13; EL/PL (brachypterous morph): 0.74–0.86, 0.80; EL/PL (macropterous morph): 0.87–1.02, 0.94; TiL/TaL: 1.11–1.29, 1.19.

Habitus as in Fig. 127. Coloration uniformly reddish yellow, with the elytra and the terminal tarsomeres usually even paler yellowish.

Head slightly transverse and wider than pronotum (see ratios HL/HW and PW/HW); puncturation coarse and moderately sparse on frons, composed of predominantly finer punctures and some scattered coarse punctures in lateral and posterior dorsal area; median dorsal area without puncturation; microsculpture shallow, but distinct. Eye size dimorphic: either small, with 7–10 distinct ommatidia (Fig. 130), weakly protruding from lateral contours of head (Fig. 128), or larger, with approximately 30 ommatidia (Fig. 131), distinctly convex and protruding from lateral contours of head (Fig. 129). Antenna as in Fig. 132. Maxillary palpus rather short, preapical joint



Figs. 127–141. *Micrillus torretassoi* (Koch) from Egypt (lectotype: 127–128, 130, 132, 137; paralectotypes: 135, 138–139, 141) and Sudan (129, 131, 133–134, 136, 140). – **127**. Habitus. **128–129**. Forebody. **130–131**. Head in lateral view. **132**. Antenna. **133**. Male tergite VIII. **134**. Male sternite VIII. **135**. Posterior part of male sternite VIII. **136**. Male abdominal segments IX–X. **137–141**. Aedeagus in lateral and ventral view. – Scale bars: 1.0 mm (127–129), 0.5 mm (130–132), 0.2 mm (133–134, 136–141), 0.1 mm (135).

little more than twice as long as wide, apical joint slightly less than half the length of preapical joint and of distinctly conical shape.

Pronotum moderately oblong (see ratio PL/PW) and moderately tapering caudad (Figs. 128–129); posterior margin weakly concave; puncturation moderately sparse and extremely fine, sometimes barely noticeable; microsculpture absent.

Elytra dimorphic, in brachypterous morph approximately 1.1 times as wide as and at suture distinctly shorter

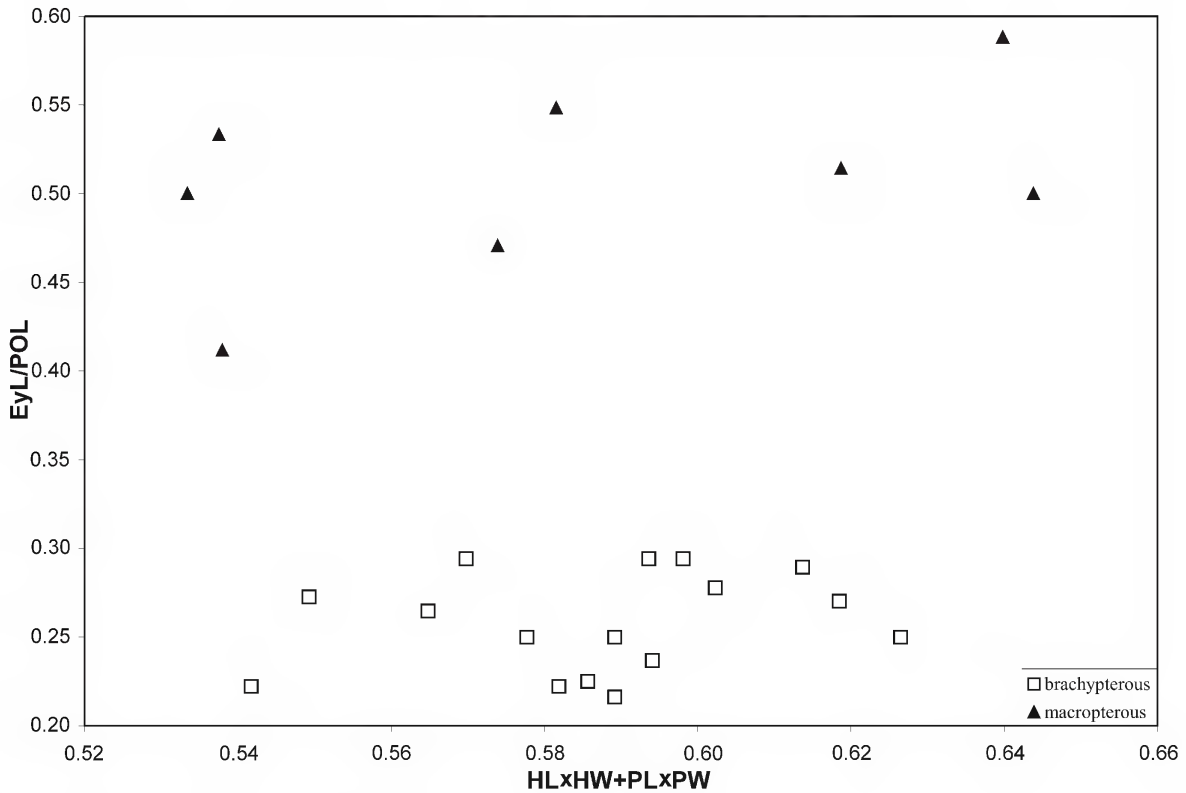


Fig. 142. *Micrillus torretassoi* (Koch). Relative eye size (EyL/POL) in relation to body size.

than pronotum (see Fig. 128 and ratio EL/PL), in macropterous morph approximately 1.2 times as wide and almost as long as pronotum (see Fig. 129 and ratio EL/PL); puncturation fine, dense and shallow. Hind wings either of reduced length or fully developed.

Legs rather short; metatarsomere I approximately as long as the combined length of II+III, sometimes slightly longer.

Abdomen in brachypterous morph as wide as or slightly wider than elytra, in macropterous morph as wide as or slightly narrower than elytra; widest at segments V–VI; puncturation moderately dense and moderately fine, somewhat sparser on posterior than on anterior tergites; posterior margin of tergite VII in brachypterous morph with narrow rudiment of palisade fringe, in macropterous morph with fully developed palisade fringe; posterior margin of tergite VIII strongly convex (Fig. 133).

♂: sternite VII unmodified; shape of sternite VIII distinctive, posterior margin in the middle deeply and very narrowly incised, this incision almost reaching middle of sternite (Figs. 134–135); valvulae of segment IX much shorter than in *M. aegyptiacus* (Fig. 136); aedeagus asymmetric and with internal structures of distinctive morphology (Figs. 137–141).

Intraspecific variation

Maximum/minimum ratios: AL: 1.33; EyL (total): 2.50; EyL (brachypterous morph): 1.38; EyL (macropterous morph): 1.43; POL (total): 1.33; POL (brachypterous morph): 1.21; POL (macropterous morph): 1.17; HL: 1.12; HW: 1.10; PW: 1.11; PL: 1.12; EL (brachypterous morph): 1.10; EL (macropterous morph): 1.27; TiL: 1.20; TaL: 1.25; ML: 1.09; TL: 1.19; EyL/POL (brachypterous morph): 1.36; EyL/POL (macropterous morph): 1.43; HL/HW: 1.18; PW/HW: 1.12; PL/PW: 1.05; EL/PL (brachypterous morph): 1.16; EL/PL (macropterous morph): 1.18; TiL/TaL: 1.17.

The species is characterised by a pronounced dimorphism of eye size, head shape, the length of the elytra, and the length of the hind wings. In the macropterous morph, the eyes are distinctly larger, composed of numerous ommatidia, and distinctly protruding from the lateral contours of the head (Figs. 129, 131), the head is approximately as long as wide, and the elytra are larger and approximately as long as the pronotum or slightly shorter. In the brachypterous morph, in contrast, the eyes are much smaller (Figs. 128, 130), composed of only few ommatidia, and not distinctly visible in dorsal view, the head is more or less transverse, and the elytra are narrower and dis-

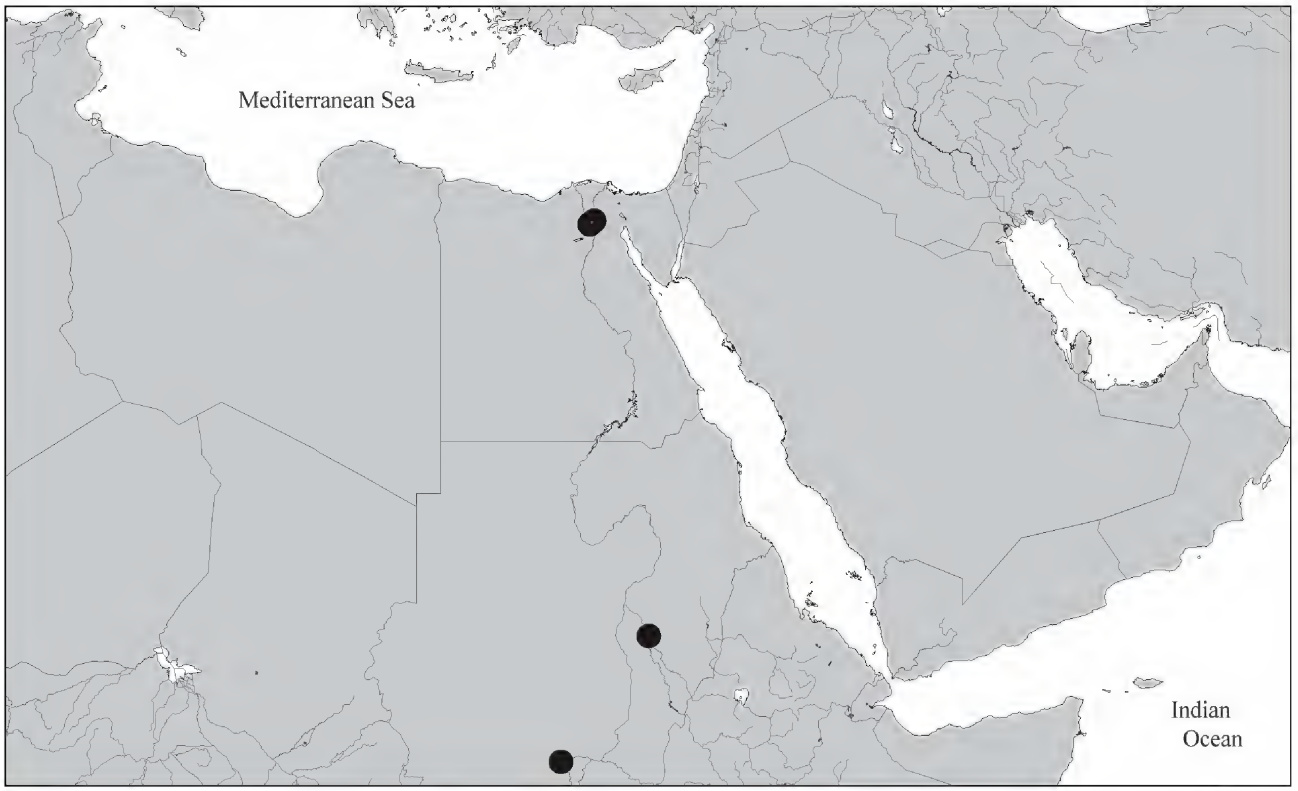


Fig. 143. Distribution of *Micrillus torretassoi* (Koch), based on examined records.

tinctly shorter than the pronotum. The macropterous morph has become known only from Sudan, whereas the distribution of brachypterous populations seems to be confined to Egypt.

Comparative notes

From all other *Micrillus* species occurring in the Palaearctic region, *M. torretassoi* is distinguished by its distinctly smaller size and by the distinctive morphology of the male primary and secondary sexual characters, especially the deeply and narrowly incised sternite VIII and the complex morphology of the aedeagus. *Micrillus aegyptiacus*, the only other congener recorded from Egypt, is much larger, and has much longer antennae, larger eyes, longer elytra, fully developed hind wings, and longer legs; for comparison, see the measurements in the section on *M. aegyptiacus*.

Distribution and bionomics

The species is currently known from Egypt and Sudan (Fig. 143). The material was collected in the surroundings of Cairo in September and October and in Sudan in March and October. The specimens from Wad Medani were found at a light source, suggesting that the species may be capable of long-distance dispersal by flight.

3.2.11 *Micrillus indicus* (Eppelsheim, 1890) (Figs. 126, 144–153)

Scymbalium indicum Eppelsheim, 1890: 277 f.

Type material examined

Syntypes?: 3 exs.: "India or., Nagpore" (MNHUB).

Comments

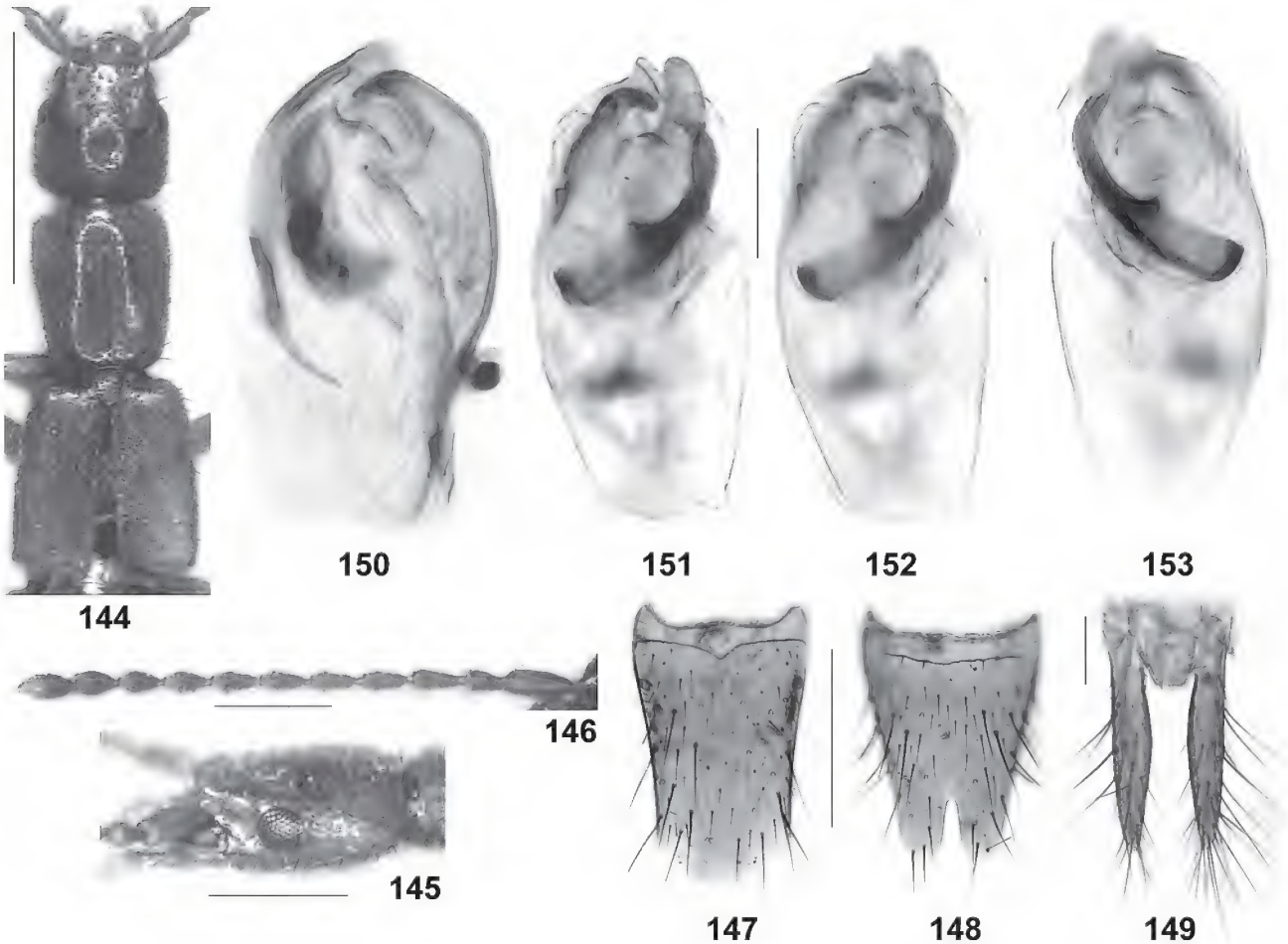
The original description is based on numerous syntypes ("a D. Dr. Bomford … pluries captum") from "India centrali … prope Nagpore" (Eppelsheim 1890). The above specimens are from the type locality, but their type status is uncertain.

Diagnosis

Similar in external appearance (size, proportions, coloration) to *M. irakensis*, but distinguished as follows:

Posterior margin of head truncate, not concave (Fig. 144); eyes slightly smaller (see measurements and Fig. 145). Antenna as in Fig. 146. Pronotum with distinctly less dense puncturation (Fig. 144). Tarsi more slender; metatarsomere I slightly longer than the combined length of II+III.

♂: tergite VIII as in Fig. 147; posterior margin of ster-



Figs. 144–153. *Micrillus indicus* (Eppelsheim). – **144**. Forebody. **145**. Head in lateral view. **146**. Antenna. **147**. Male tergite VIII. **148**. Male sternite VIII. **149**. Male abdominal segments IX–X. **150–153**. Aedeagus in lateral (150), ventral (151–152) and dorsal view (153). – Scale bars: 1.0 mm (144), 0.5 mm (145–148), 0.2 mm (149), 0.1 mm (150–153).

nite VIII with deep and narrow incision (Fig. 148); valvulae of segment IX very long (Fig. 149); aedeagus small and of distinctive complex morphology (Figs. 150–153).

Distribution

The species is known only from India (Fig. 126).

3.2.12 *Micrillus sudanicus* **n. sp.** (Figs. 126, 154–163)

Type material

Holotype ♂: "Sudan, Wad Medani, a. Bl. Nil, 18.X.1979, lux, leg. F. Hieke / Holotypus *Micrillus sudanicus* sp. n. det. V. Assing 2007" (MNHUB).

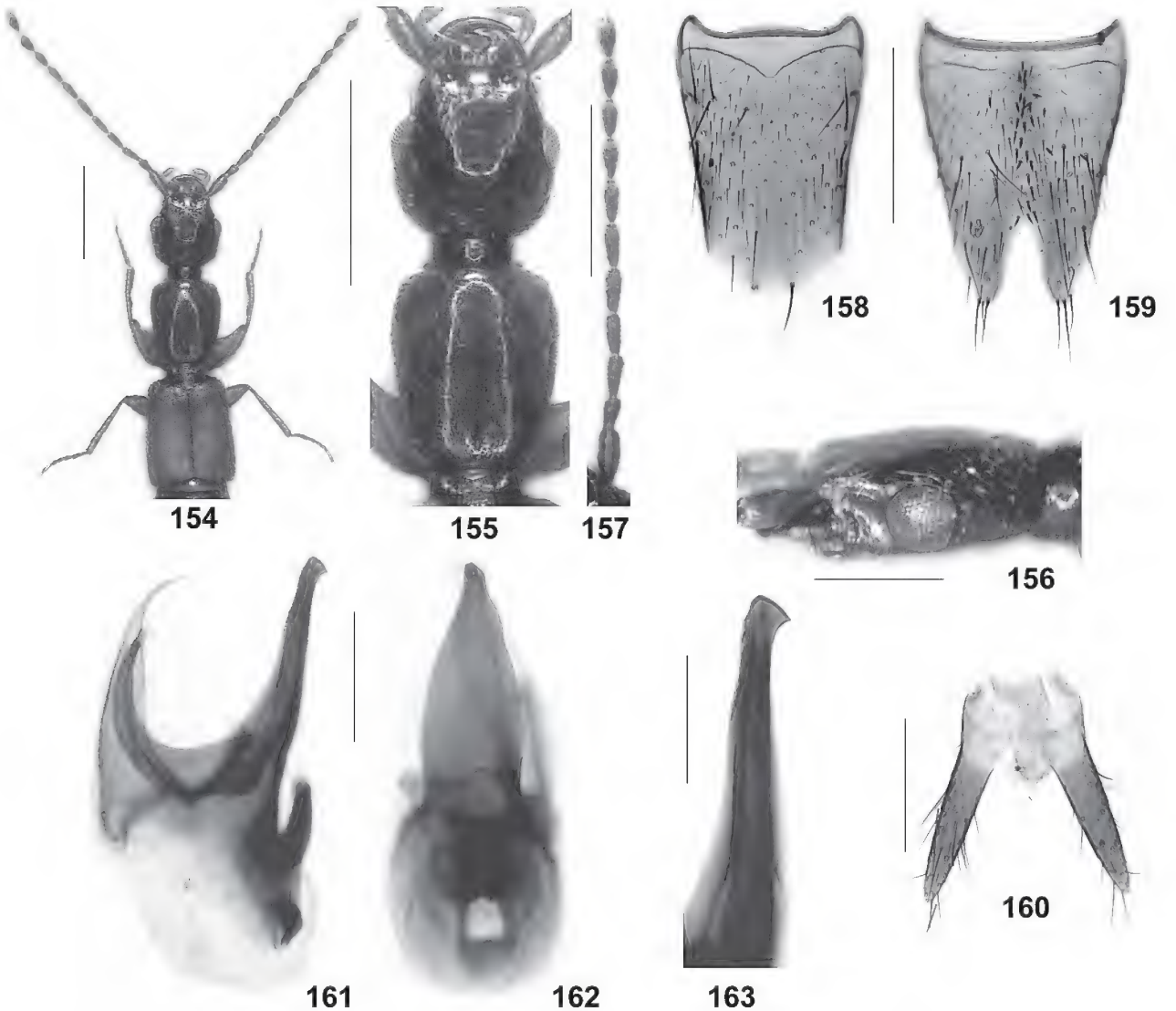
Paratypes: 2 ♀♀: same data as holotype, but 12.X.1979 (MNHUB); 1 ♂: same data, but 14.X.1979 (MNHUB); 1 ♂: same data, but 15.X.1979 (MNHUB); 1 ♂, 2 ♀♀: same data, but 20.X.1979 (MNHUB, cAss); 1 ♀: same data, but 22.X.1979 (MNHUB); 1 sex?: same data, but 24.X.1979 (MNHUB); 3 ♂♂: same data, but 26.X.1979 (MNHUB, cAss); 1 ♂, 1 ♀: same data, but 30.–31.X.1979 (MNHUB, cAss); 1 ♀: "Sudan, Wad Medani, a. Bl. Nil, 18.X.1979, lux, leg. Königsmann" (MNHUB); 1 ♀: "Sudan, Senaar a. Bl. Nil, lux, 21.X.1979, leg. Hieke" (MNHUB).

Etymology

The name (adj.) is derived from Sudan, where all the localities are situated.

Description

Measurements (in mm) and ratios (range, arithmetic mean; n = 17): AL: 2.50–2.81, 2.64; EyL: 0.21–0.29, 0.26; POL: 0.27–0.35, 0.30; HL: 0.79–0.85, 0.82; HW: 0.76–0.85, 0.81; PW: 0.75–0.87, 0.81; PL: 0.88–0.99, 0.94; EL: 0.86–1.00, 0.93; TiL: 0.79–0.86, 0.83; TaL: 0.66–0.77, 0.70; ML: 0.68–0.74, 0.71; TL: 4.9–5.7, 5.3; EyL/POL: 0.70–1.06, 0.86; HL/HW: 0.98–1.05, 1.02; PW/HW: 0.96–1.05, 1.01;



Figs. 154–163. *Micrillus sudanicus* n. sp. – **154**. Forebody. **155**. Head and pronotum. **156**. Head in lateral view. **157**. Antenna. **158**. Male tergite VIII. **159**. Male sternite VIII. **160**. Male abdominal segments IX–X. **161–162**. Aedeagus in lateral and ventral view. **163**. Apex of ventral process of aedeagus in lateral view. – Scale bars: 1.0 mm (154–155, 157), 0.5 mm (156, 158–160), 0.2 mm (161–162), 0.1 mm (163).

PL/PW: 1.13–1.18, 1.16; EL/PL: 0.95–1.05, 1.00; TiL/TaL: 1.10–1.24, 1.18.

Habitus of forebody as in Fig. 154. Head reddish brown to blackish brown; pronotum reddish to castaneous brown; elytra reddish to reddish yellow; abdomen reddish brown; legs yellowish brown; antennae reddish.

Head approximately as wide as long (see ratio HL/HW and Fig. 155); puncturation fine and moderately dense; median dorsal area impunctate or with very sparse puncturation; microsculpture transverse, extremely shallow and fine. Eyes relatively large (see ratio EyL/POL and Fig. 156) and distinctly projecting from lateral contours of head in dorsal view (Fig. 155). Antenna long and slender (Fig. 157). Maxillary palpus with the terminal joint approximately half as long as preapical joint, distinctly coniform, sometimes somewhat flattened.

Pronotum approximately as wide as head, and distinctly oblong (see ratios PW/HW and PL/PW); posterior margin weakly concave; predominant puncturation fine and rather dense, interstices on average approximately as wide as punctures or narrower (Fig. 155); median impunctate area very narrow or indistinct; on either side of midline with row of approximately five coarse punctures.

Elytra relatively long (see ratio EL/PL), with parallel

lateral margins, and with well-developed humeral angles; puncturation fine, very dense, shallow, and ill-defined; microsculpture very shallow or indistinct. Hind wings fully developed.

Legs slender; metatarsomere I usually slightly longer than the combined length of II+III.

Abdomen slightly (0.90–0.95×) narrower than elytra, widest at segment V; puncturation very dense; surface with distinct microsculpture; posterior margin of tergite VII with palisade fringe; posterior margin of tergite VIII strongly convex (Fig. 158).

♂: sternite VII unmodified; sternite VIII along middle with modified short stout dark setae, posterior margin deeply and rather narrowly incised (Fig. 159); valvulae of segment IX conspicuously long, more than 3 times as long as tergite X (Fig. 160); aedeagus moderately asymmetric, of distinctive morphology (Figs. 161–163).

Intraspecific variation

Maximum/minimum ratios: AL: 1.12; EyL: 1.36; POL: 1.28; HL: 1.09; HW: 1.12; PW: 1.16; PL: 1.13; EL: 1.16; TiL: 1.10; TaL: 1.16; ML: 1.09; TL: 1.16; EyL/POL: 1.51; HL/HW: 1.07; PW/HW: 1.09; PL/PW: 1.04; EL/PL: 1.11; TiL/TaL: 1.13.

Except for the highly variable relative and absolute eye size, morphological characters are subject to moderate intraspecific variation.

Comparative notes

Based on external and the male sexual characters, *M. sudanicus* is closely related to *M. aegyptiacus*. From this species, *M. sudanicus* is readily distinguished by the darker and relatively smaller head, by larger and more bulging eyes, the denser puncturation of pronotum and abdomen, the completely different shape and chaetotaxy of the male sternite VIII, as well as by the distinctive morphology of the aedeagus. From *Scymbalium usagarae* Bernhauer, the new species is separated by the darker head, the much denser puncturation of the pronotum and by the different shape of the aedeagus. For illustrations of the primary sexual characters of *S. usagarae* and other species of *Scymbalium* described from the Ethiopian region and possibly referring to *Micrillus* see FAGEL (1960).

Distribution and bionomics

The species was discovered in two localities near Wad Medani near or on the bank of the Blue Nile (Fig. 126). The specimens were collected at a light source in October.

3.3 Key to the species of *Micrillus*

1 Apical joint of maxillary palpus long and slender, at least half the length of preapical palpomere (Fig. 39). Aedeagus of simple morphology, usually slender with ventral process apically more or less bent dorsad; internal structures amorphous and weakly sclerotised. – Western Palaearctic (including Middle Asia); absent from Egypt (Fig. 2). *Micrillus testaceus* group. **2**

– Apical joint of maxillary palpus of conical shape and shorter than half the length of preapical palpomere. Aedeagus of complex morphology, usually asymmetric and with distinctly sclerotised internal structures. – Afrotropical and Oriental regions, in the Palaearctic confined to Egypt (Fig. 2). *Micrillus aegyptiacus* group. **9**

2 Eyes fully developed or of reduced size, but always composed of ommatidia. Posterior margin of abdominal tergite VII at least with narrow rudiment of a palisade fringe. . . . **3**

– Eyes extremely reduced, without ommatidia. Abdominal tergite VII without palisade fringe. – Distribution confined to North Africa. **7**

3 Posterior margin of head distinctly concave in the middle (Fig. 61). Eyes, elytra, and hind wings not reduced (Figs. 59–60, 62). Posterior margin of male sternite VIII with deeply and broadly triangular excision (Fig. 64). Aedeagus as in Figs. 66–74. – Known distribution confined to Iraq and Israel (Fig. 58). . . . . ***M. irakensis*** (Cameron)

– Posterior margin of head not distinctly concave, usually truncate. Aedeagus of different morphology. **4**

4 Species of pale (yellowish, reddish or pale brown) coloration. Eyes, elytra, and hind wings not reduced (Figs. 48–49). Posterior margin of male sternite VIII with shallow emargination (Fig. 50). Aedeagus of distinctive shape, rather broad in ventral view, ventral process apically not bent dorsad, and with two clusters of moderately sclerotised internal structures (Figs. 51–55). – Caucasus region and Middle Asia (Fig. 58). . . . . ***M. pallidus*** (Reitter)

– Mature specimens usually (but not always!) of darker coloration, reddish to dark brown. Eyes, elytra, and hind wings often of reduced size or length, respectively. Aedeagus more slender, with one cluster of internal structures and with ventral process apically bent dorsad. **5**

5 Wing-dimorphic, on average smaller species; eyes on average larger (EyL/POL: 0.23–0.55). Elytra and abdomen with finer puncturation (Figs. 4–9, 11). Posterior margin of male sternite VIII with deeper triangular emargination (Fig. 13). Widespread species with slender aedeagus with more weakly sclerotised ventral process (Figs. 16–26), or distribution confined to Algeria. **6**

– Monomorphic brachypterous species (Figs. 34–35); eyes (Fig. 38) usually smaller (EyL/POL: 0.21–0.33). Elytra and abdomen with coarser and denser puncturation (Figs. 35, 37). Posterior margin of male sternite VIII with shallow emargination (Fig. 56). Aedeagus relatively broad and with rather strongly sclerotised ventral process (Figs. 41–46). – Endemic to northern Morocco (Fig. 47). . . . . ***M. scabrosus*** (Fauvel)

6 Aedeagus longer (> 0.75 mm), slender, and with weakly sclerotised internal structures (Figs. 16–26). – Widespread in the south of the West Palaearctic region (Fig. 32). . . . . ***M. testaceus*** (Erichson)

– Aedeagus shorter (< 0.70 mm), broader, and with distinctly sclerotised internal structures (Figs. 106–110). – Known only from the surroundings of Biskra, Algeria (Fig. 47). . . . . ***M. biskrensis*** (Fauvel)

7 Elytra slightly narrower than pronotum (Fig. 98). Eye rudiments (Fig. 99) slightly larger, 0.06–0.07 mm, EyL/POL: 0.12–0.15. Aedeagus apically pointed in ventral view (Figs. 102–103). – Known only from two localities in Taza district, Morocco (Fig. 47). . . . . ***M. tenuipennis*** **n. sp.**

– Elytra approximately as wide as pronotum. Eye rudiments

(Figs. 77, 88) smaller, 0.03–0.05 mm, EyL/POL: 0.07–0.13. Aedeagus apically weakly to distinctly concave in ventral view. – Distribution confined to Algeria. **8**

8 Smaller species; HL < 0.80 mm, HW < 0.80 mm, PW < 0.80 mm. Antenna shorter (Fig. 89), AL < 2.05 mm. Eye rudiments smaller (Fig. 88), EyL: 0.03–0.05 mm. Pronotum on average more oblong (Fig. 87), PL/PW: 0.12–0.17. Head less oblong (Fig. 87), HL/HW: 0.97–1.02, and smaller in relation to pronotum, approximately as wide as pronotum (Fig. 87), PW/HW: 0.97–1.02. Head with coarser and denser puncturation and with more pronounced microsculpture (Fig. 87). Aedeagus apically weakly concave in ventral view and less strongly bent dorsad in lateral view (Figs. 93–96). – Algeria: surroundings of Algier (Fig. 47). . ***M. subterraneus*** Raffray

– Larger species; HL ≥ 0.90 mm, HW > 0.85 mm, PW > 0.80 mm. Antenna longer (Fig. 78), AL > 2.15 mm. Eye rudiments slightly larger (Fig. 77), EyL: 0.05 mm. Pronotum on average less oblong (Fig. 76), PL/PW: 0.10–0.13. Head more oblong (Fig. 76), HL/HW: 1.03–1.08, and larger in relation to pronotum, wider than pronotum (Fig. 76), PW/HW: 0.90–0.97. Head with finer and sparser puncturation and with weaker microsculpture (Fig. 76). Aedeagus apically distinctly concave in ventral view and strongly bent dorsad in lateral view (Figs. 81–85). – Algeria: Djebel Bou Zegza (Fig. 47). . . . . ***M. hypogaeus*** (Peyerimhoff)

9 Smallest species of the genus; HL < 0.60 mm, HW < 0.60 mm, PL < 0.65 mm, PW < 0.55 mm. Wing-dimorphic (Figs. 128–129); brachypterous morph with very small eyes (Fig. 130), short elytra, and reduced hind wings (Fig. 128). Valvulae of abdominal segment IX relatively short (Fig. 136). Male sternite VIII posteriorly very deeply and very narrowly incised (Figs. 134–135). Aedeagus of distinctive morphology (Figs. 130–134). – Egypt and Sudan (Fig. 143). . . . . ***M. torretassoi*** (Koch)

– Larger species; HL > 0.70 mm, HW > 0.70 mm, PL > 0.80 mm, PW > 0.65 mm. Monomorphic macropterous species with distinctly larger eyes. Valvulae of abdominal segment IX very long. Male sternite VIII posteriorly with much less deep and broader excision. Aedeagus of completely different morphology. **10**

10 Eyes smaller (Fig. 145). Male sternite VIII posteriorly more deeply and more narrowly incised (Fig. 148). Aedeagus of distinctive morphology (Figs. 150–153). – India (Fig. 126). . . . . ***M. indicus*** (Eppelsheim)

– Eyes larger. Male sternite VIII and aedeagus of different morphology. – Africa. **11**

11 Eyes larger and more bulging (Figs. 155–156). Head shorter, HL 0.79–0.85 mm. Pronotum (Fig. 155) and abdomen with very dense puncturation. Male sternite VIII with short stout modified setae in the middle and with pronounced posterior excision (Fig. 159). Aedeagus of distinctive morphology (Figs. 161–163). – Sudan (Fig. 126). . . . . ***M. sudanicus*** **n. sp.**

– Eyes somewhat smaller and less bulging (Figs. 112–113). Head longer, HL 0.88–0.94 mm. Pronotum (Fig. 112) and abdomen with less dense puncturation. Male sternite VIII without modified setae and with broader and less deep posterior excision (Fig. 116). Aedeagus of completely different morphology (Figs. 118–123). – Egypt (Fig. 126). . . . . ***M. aegyptiacus*** (Bernhauer)

3.4 Synonymic catalogue

The species names are listed in alphabetic order in Tab. 1; species from regions other than the Palaearctic are given in square brackets. The distribution is based exclusively on examined material.

3.5 On the identity of *Scymbalium minimum* Eppelsheim

The species, which was originally described from "Macedonien" (Eppelsheim 1888), has been listed in the catalogues by Bernhauer & Schubert (1912) and Smetana (2004), and was also included in the key to the species of *Scymbalium* by Wanka (1914), but has never been recorded again. Since, with few exceptions, all the *Micrillus* species described before 1980 were originally described in *Scymbalium*, it did not seem unlikely that *S. minimum*, too, should belong to *Micrillus*. An examination of the types, however, revealed that they refer to neither of the two genera, but to the following species of the genus *Pseudomedon*:

Pseudomedon dido (Saulcy, 1865)

Scymbalium minimum Eppelsheim, 1888 408 f.; **n. syn.**
Medon apfelbecki Bernhauer, 1899: 25; synonymy confirmed.

Type material examined

S. minimum: Holotype ♂: "Macedon. / 26 / minimum Epp., Deutsch. ent. Zeit. 1888, p. 408 / Typus / c. Epplsh. Steind. d. / Holotypus *Scymbalium minimum* Eppelsheim rev. V. Assing 2007 / *Pseudomedon dido* (Saulcy) det. V. Assing 2007" (NHMW).

M. apfelbecki: Lectotype ♂, here designated: "Sarajevo, Hochwass / *Apfelbecki* Bernh. Type / *Medon Apfelbecki* Typus / Lectotypus *Medon apfelbecki* Bernhauer desig. V. Assing 2007 / *Pseudomedon dido* (Saulcy) det. V. Assing 2007" (NHMW). – Paralectotype [abdomen missing]: "Hochwasser / *Apfelbecki* Bernh. Bosn., Apfelb. Type / Typus" (NHMW).

Additional material examined

Bosnia-Herzegovina: 1 ex., Ilidže, 1902, leg. Apfelbeck (NHMW); 1 ex., Sarajevo, leg. Apfelbeck (NHMW).

Comments

The original description of *Scymbalium minimum* is explicitly based on a single specimen from "Macedonien" (Eppelsheim 1888). An examination of the aedeagus revealed that it is conspecific with the current interpretation of *Pseudomedon dido*.

Bernhauer (1899) based the original description of *Medon apfelbecki* on several specimens ("in mehreren Stücken" from the "Umgebung von Sarajevo in Bosnien". Two of these syntypes, one of them a male in good condition and the other a specimen without abdomen, were found in the collections of the NHMW. The male is here designated as the lectotype.

Tab. 1. Synonymic catalogue of *Micrillus* spp.

Species	Distribution
aegyptiacus (Bernhauer, 1910) = *bernhaueri* (Koch, 1934); **n. syn.**	Egypt
biskrensis (Fauvel, 1898)	Algeria
hypogaeus (Peyerimhoff, 1907)	Algeria
[*indicus* (Eppelsheim, 1890)]	India
irakensis (Cameron, 1940)	Iraq, Israel
pallidus (Reitter, 1887) = *rufotestaceus* (Cameron, 1939) = *caucasicus* Coiffait, 1980; **n. syn.**	Armenia, Azerbaijan, Russian South European territory, Uzbekistan, Turkmenistan
scabrosus (Fauvel, 1875)	Morocco
subterraneus Raffray, 1873	Algeria
[*sudanicus* **n. sp.**]	Sudan
tenuipennis **n. sp.**	Morocco
testaceus (Erichson, 1840) = *grandiceps* (Jacquelin du Val, 1853); **resyn.** = *longicollis* (Mulsant & Rey, 1853) = *pubipennis* Fairmaire, 1860); **n. syn.** = *longipennis* (Brisout, 1863); **n. syn.** = *saintpierrei* (Allard, 1869) = *trapezicollis* (Uhagón, 1876) = *meridionalis* (Gridelli, 1914) = *tergestina* (Gridelli, 1914); **n. syn.** = *zuercheri* (Wanka, 1914); **n. syn.** = *libanicus* Coiffait, 1980; **n. syn.** = *hispanicus* Coiffait, 1980; **n. syn.** = *zacinthicus* Coiffait, 1980; **n. syn.** = *syriacus* Coiffait, 1980; **n. syn.** = *calabricus* Coiffait, 1980; **n. syn.** = *turcicus* Coiffait, 1980; **n. syn.** = *graecus* Coiffait, 1980; **n. syn.** = *cypriacus* Coiffait, 1980; **n. syn.** = *corcyranus* Coiffait, 1980; **n. syn.** = *brekhovi* Grebennikov, 2001; **n. syn.**	Mediterranean region: Tunisia, Algeria, Morocco, Gibraltar, Spain, Portugal, France, Italy, Croatia, Bosnia-Herzegovina, Montenegro, Albania, Greece, Turkey, Cyprus, Lebanon, Syria, Israel; Ukraine, southwest of Russian Federation (Russian South European territory)
torretassoi (Koch, 1934) = *collare* (Scheerpeltz, 1962); **n. syn.**	Egypt, Sudan

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Manuscript received: 9.V.2007, accepted: 18.VII.2007.

Revision der paläarktischen Arten der Gattung *Brachygluta* (Coleoptera: Staphylinidae: Pselaphinae) – Nachträge zum 1. Teil

Revision of the Palaearctic species of the genus *Brachygluta* (Coleoptera: Staphylinidae: Pselaphinae) – Additions to part 1

Christoph Bückle & Volker Brachat

Abstract

A new species from Kazakhstan, *Brachygluta kazakhica* **n. sp.**, and a new subspecies from Libanon and Turkey, *Brachygluta foveola symmetrica* **n. ssp.**, are described. External morphology and aedeagus of *Brachygluta kurdica* Besuchet, 2004 are figured.

Keywords: Coleoptera, Staphylinidae, Pselaphinae, *Brachygluta*, new species, new subspecies.

Zusammenfassung

Eine neue Art aus Kasachstan, *Brachygluta kazakhica* **n. sp.**, und eine neue Unterart aus dem Libanon und der Türkei, *Brachygluta foveola symmetrica* **n. ssp.**, werden beschrieben. Merkmale der äußeren Morphologie und der Aedeagus von *Brachygluta kurdica* Besuchet, 2004 werden abgebildet.

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1 Einleitung

Nach Fertigstellung des ersten Teils der Revision der paläarktischen *Brachygluta*-Arten (Sabella et al. 2004) stießen die Autoren im Material des Staatlichen Museums für Naturkunde in Stuttgart auf einige Exemplare einer bisher unbekannten, der *nodiventris*-Gruppe angehörenden *Brachygluta*-Art aus Kasachstan, also vom – soweit bisher bekannt – östlichen Randbereich des Areals der Gattung. Dieses Taxon wird unten beschrieben.

In der erwähnten Revision (Sabella et al. 2004: Abb. 275–278, 587–590) hatten die Autoren bei der Beschreibung von *Brachygluta foveola* (Motschulsky, 1840) auf drei Männchen aus der Küstenregion des östlichen Mittelmeerraumes hingewiesen, die zwar hinsichtlich ihrer äußeren morphologischen Merkmale von *B. foveola* nicht sicher abzugrenzen waren, aber einen deutlich abweichenden Bau des Aedeagus aufwiesen. Ein weiteres Männchen, aufgefunden an der Südküste der Türkei bei Mersin, welches gänzlich mit den oben erwähnten Exemplaren übereinstimmt, hat uns nun davon überzeugt, dass es sich um eine im männlichen Geschlecht von der Stammform gut abgegrenzte neue Unterart handelt, deren Verbreitung der östliche Mittelmeerraum ist.

Die Art *B. kurdica* Besuchet war uns seinerzeit so spät bekannt geworden, dass in der Arbeit von 2004 nur eine Beschreibung ohne die dazugehörigen Abbildungen möglich war. Diese Abbildungen (Abb. 6–9) werden hier nachgeliefert.

Abkürzungen der Sammlungen

MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
PCVB	Private Sammlung Volker Brachat, Geretsried
SMNS	Staatliches Museum für Naturkunde, Stuttgart

Dank

Herrn Dr. W. Schawaller (SMNS) danken wir für die Überlassung des Materials zur Beschreibung und die Angaben zum Fundort.

2 *Brachygluta kazakhica* n. sp.

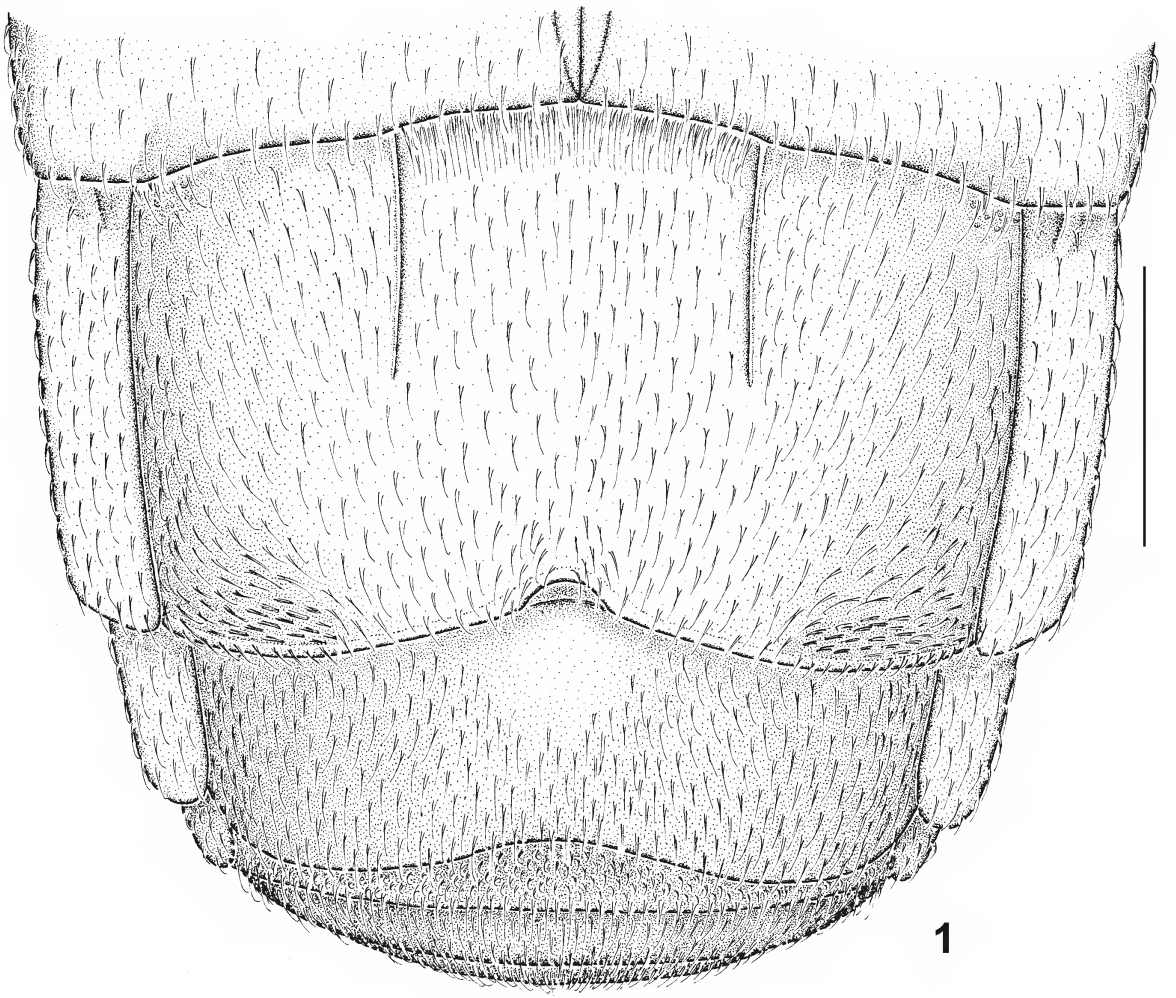
Holotypus (♂): SE Kazakhstan, Charyn Valley, W Chundzha, 800 m, 10.–13.VI.1993, leg. W. Schawaller (SMNS).

Paratypen: 1 ♂, 2 ♀♀, gleiche Funddaten wie der Holotypus (SMNS). 1 ♂, SE Kazakhstan, Charyn Canyon, W Chundzha, 650 m, 29.–31.V.2001, leg. W. Schawaller (SMNS).

Beschreibung

Körperlänge 1,7–1,8 mm.

Färbung und Behaarung: Rötlichbraun, Bei-



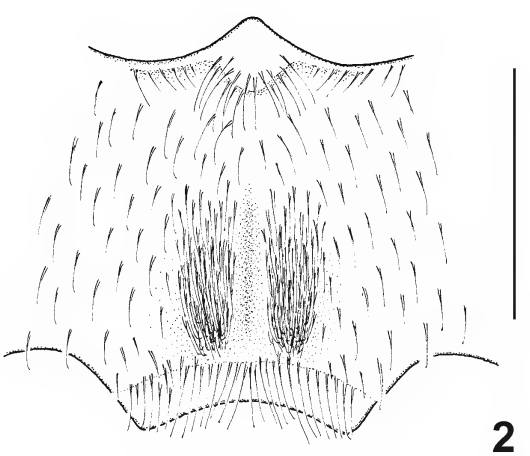


Abb. 1–2. *Brachygluta kazakhica* n. sp., Holotypus (♂). – **1**. Sichtbarer Teil des Abdomens dorsocaudal. **2**. Metasternum. – Maßstab: 0.2 mm.

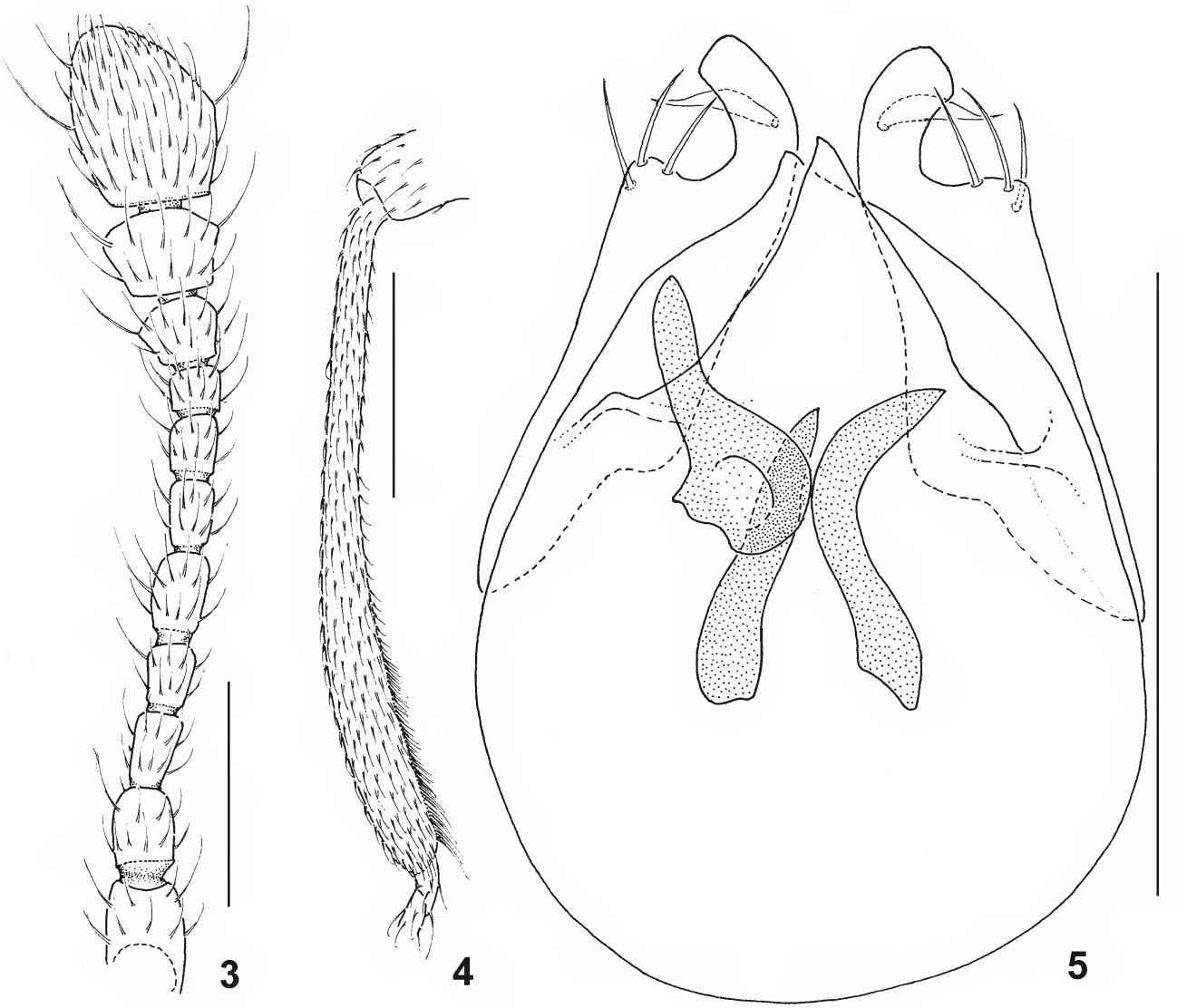


Abb. 3–5. *Brachygluta kazakhica* n. sp., Holotypus (♂). – **3**. Antenne rechts. **4**. Hintertibia rechts anterior. **5**. Aedeagus dorsal. – Maßstab: 0.2 mm.

ne und Palpen etwas heller; glänzend mit spärlicher, feiner Punktierung; Behaarung gelblich, fast anliegend, mit einzelnen paarweise angeordneten und mehr aufgerichteten Haaren auf Kopf und Pronotum.

Kopf $^1/_9$–$^1/_7$ breiter als lang; Augen groß, stark hervortretend, ihr Durchmesser übertrifft die Länge der schwach konvexen Schläfen. Scheitelfossetten deutlich, am Grunde tomentiert, die hinteren dem Innenrand der Augen stark genähert, Abstand zum Augenrand geringer als der Durchmesser der Fossette; Scheitel vor dem Hinterrand mit medianem Längskielchen.

Antennen (Abb. 3) gestreckt. Scapus und Pedicellus deutlich länger als breit; 3., 5. und 6. Antennenglied gut 1,5 mal so lang wie breit; 4. u. 7. nicht ganz 1,5 mal so lang wie breit; 8. quadratisch; 9. wenig breiter als lang; 10. deutlich breiter als lang; 11. deutlich ($^1/_3$) länger als breit.

Pronotum $^1/_6$ breiter als lang, etwa so lang wie der Kopf und deutlich breiter als dieser, etwas vor der Längsmitte am breitesten; Diskus konvex; Fossetten groß, die lateralen dem Seitenrand genähert.

Elytren $^1/_3$ (♂) bis $^2/_5$ (♀) breiter als lang, im distalen Drittel am breitesten, zur deutlichen Schulterbeule gleichmäßig gerundet verjüngt; Dorsalstreifen $^3/_4$ bis $^4/_5$ der Länge der Elytren erreichend.

Abdomen etwa so lang wie die Elytren (♀), beim ♂ in Ansicht senkrecht auf das erste Tergit deutlich kürzer. 1. sichtbares Tergit $^2/_3$ breiter als lang; Basalcarenulae gerade oder leicht nach außen gebogen, etwa $^2/_5$ der Tergit-

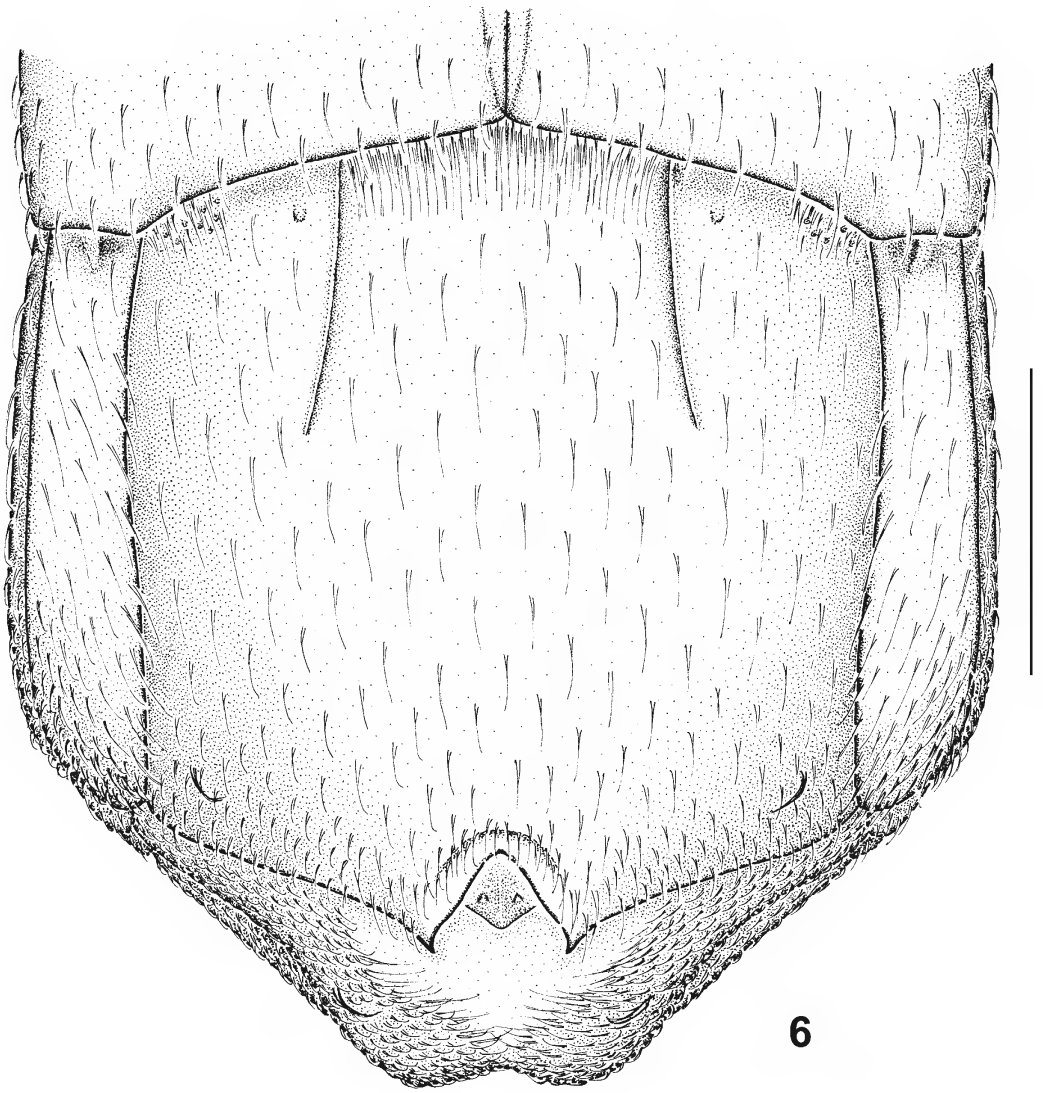


Abb. 6. *Brachygluta kurdica* Besuchet, Holotypus (♂), sichtbarer Teil des Abdomens dorsocaudal. – Maßstab: 0.2 mm.

breite einschließend und die Hälfte oder gut die Hälfte der Tergitlänge erreichend.

M ä n n c h e n : 1. sichtbares Tergit gegenüber Paratergit deutlich erhöht, im mittleren Bereich abgeflacht. Distalbereich schwach nach hinten verlängert; Distalrand median niedergedrückt mit kleinem halbkreisförmigem Ausschnitt. Seitenbereiche vor dem Distalrand mit einer kleinen, dicht punktierten und kurz behaarten ovalen Fläche. 2. Tergit stärker punktiert, gut 2 mal so breit wie lang, gegenüber Paratergit deutlich erhöht; median mit einem flachen, halbkreisförmigen Eindruck, der vom Vorderrand ausgehend $^2/_3$ der Tergitlänge erreicht. Von der Mitte des Vorderrandes ragt eine kleine dreieckige, an den Seiten mit einem dichten Haarkranz versehene Lamelle nach vorne; diese ist gänzlich unter dem Distalrand des 1. Tergits verborgen und lediglich bei Trennung der Tergite zu sehen. Distalrand des 2. Tergits mit flachem, bogigem Ausschnitt im mittleren Bereich. Die weiteren Tergite stark abwärts gebogen und bei dorsaler Betrachtung vom Distalrand des 2. Tergits überdeckt und nicht sichtbar. Diskus des 3. Tergits stärker punktiert, gegenüber Paratergit deutlich erhöht, im mittleren Bereich mit flacher Depression (Abb. 1). Metasternum in der apikalen Hälfte beiderseits einer medianen Längsrinne mit einem länglichen, schräg nach hinten flach abstehenden Haarschopf (Abb. 2). Tibien (Abb. 4) ohne besondere Merkmale.

A e d e a g u s : Bei den drei der Beschreibung zugrunde liegenden Männchen wurde eine Innensackinversion nicht festgestellt. Die Innensackarmatur besteht aus drei Zähnen, wobei ein Zahn distal der verbreiterten Basis

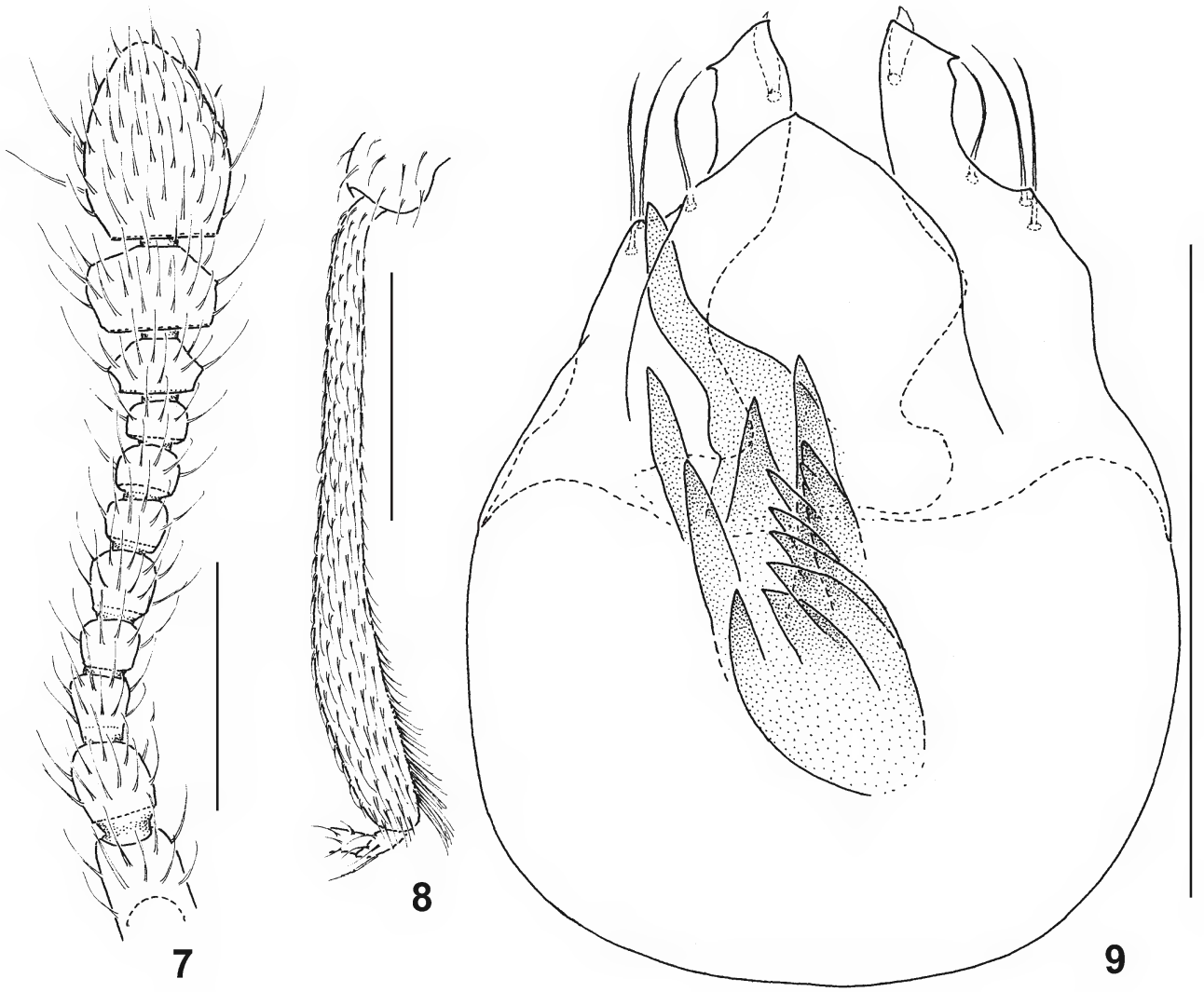


Abb. 7–9. *Brachygluta kurdica* Besuchet, Holotypus (♂). – **7**. Antenne rechts. **8**. Hintertibia rechts anterior. **9**. Aedeagus dorsal. – Maßstab: 0.2 mm.

abgeknickt und deutlich nach links gerichtet ist (Dorsalansicht, Abb. 5).

Unterscheidung von anderen Arten

Brachygluta kazakhica n. sp. steht innerhalb der *nodiventris*-Gruppe hinsichtlich der äußeren Merkmale nahe bei *B. willbergi* (Reitter, 1891); der mediane Distalbereich des 1. Tergits ist indessen bei *B. kazakhica* leicht niedergedrückt und liegt der Basis des 2. Tergits daher dichter auf, und das 2. Tergit ist in caudaler Richtung flacher gewölbt und auffällig umfangreich. Der Bau des Aedeagus ist äußerst ähnlich wie bei *B. uzbekica* Sabella, 2004 und *B. tadshikica* Sabella, 2004. Durch den kleinen medianen, halbrunden Ausschnitt am Hinterrand des 1. Tergits (Abb. 1) ist *B. kazakhica* von allen genannten Arten leicht zu unterscheiden.

Zum Fundort

Der Fluss Charyn, ein Zufluss des Ili aus dem Ketmen-Gebirge, hat eine tiefe Schlucht in eine steinige Halbwüste erodiert und wird von einem dichten Galerie-Auwald (unter anderen mit *Fraxinus potamophila*, zwei *Populus*- und mehreren *Salix*-Arten) begleitet, in dem *Brachygluta kazakhica* n. sp. gesiebt wurde. Dieser Wald wird oft überflutet, in täglichen und jahreszeitlichen Intervallen, je nach den Wetter- und Schneebedingungen in den Bergen des Oberlaufes. Die isolierte Käferfauna dieses Waldes ist auffällig artenarm. Wahrscheinlich ist dieser Wald

nur 500–1000 Jahre alt. Vor dieser Zeit war die Schlucht wesentlich höher mit Wasser gefüllt und ohne Baumbestand. In Verbindung mit der Desertifikation in historischer Zeit sank der Wasserspiegel und der Wald entwickelte sich aus Samen aus den Bergen am Oberlauf. Aber die Bodenfauna mit ihrer oft beschränkten Migrationsfähigkeit konnte diesen Ort wegen der absoluten Isolation durch die umgebende, ausgedehnte Halbwüstenregion nur in einzelnen Fällen erreichen.

3 *Brachygluta foveola symmetrica* n. ssp.

Holotypus (♂): Libanon, Beirut, ex coll. Peyron (MHNG).

Paratypen: 1 ♂, gleiche Funddaten wie der Holotypus (MHNG). 2 ♂♂, Türkei, Alexandrette [heute İskenderun] (MNHN). 1 ♂, Türkei, Mersin, S Silifke, Delta des Göksu, 36°20'N 34°1'E, 9.V.2004, leg. Meybohm & Brachat (PCVB).

Beschreibung

Körperlänge 1,45–1,55 mm.

Ausführliche Beschreibung von *Brachygluta foveola* (Motschulsky, 1840) siehe Sabella et al. (2004: 122, 123).

Unterschiede zu der Stammform

Die neue Unterart ist von der Nominatform lediglich durch Differenzen in der Morphologie des Aedeagus zu unterscheiden: Innensack mit einem großen gebogenen Zahn, Parameren symmetrisch (siehe Sabella et al. 2004: S. 227, Abb. 278); bei der Stammform ein großer gebogener sowie zwei kleinere Zähne, Parameren deutlich asymmetrisch (Sabella et al. 2004: Abb. 275).

Verbreitung

Küstengebiete des östlichen Mittelmeeres von der Südtürkei bis zum Libanon.

Ökologie

Unter pflanzlichem Anspülicht am Meeresufer.

4 Literatur

Sabella, G., Bückle, C., Brachat, V. & Besuchet, C. (2004): Revision der paläarktischen Arten der Gattung *Brachygluta* Thomson, 1859 (Coleoptera, Staphylinidae). 1. Teil: Arten mit sekundären männlichen Geschlechtsmerkmalen auf den Abdominaltergiten (Coleoptera, Staphylinidae, Pselaphinae). – Instrumenta biodiversitatis **6**: 283 S.; Genf (Muséum d'Histoire Naturelle).

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Manuskript eingegangen: 25.VI.2007, angenommen: 11.VII.2007.

The genus *Coptostethus* Wollaston from the Selvage Islands, with descriptions of two new species (Coleoptera: Elateridae)

Rainer Schimmel

Abstract

Two new species of the genus *Coptostethus*, *C. putzeri* **n. sp.**, and *C. selvagensis* **n. sp.** from the Selvage Islands are described and illustrated. *Cardiophorus (Coptostethus) oromii* Cobos, 1978 is transferred to the genus *Coptostethus*; new data on this species are recorded.

Keywords: Coleoptera, Elateridae, *Coptostethus*, Selvage Islands.

Zusammenfassung

In der vorliegenden Arbeit werden zwei neue Arten der Gattung *Coptostethus*, *C. putzeri* **n. sp.** und *C. selvagensis* **n. sp.**, von den Selvagen-Inseln beschrieben und abgebildet. *Cardiophorus (Coptostethus) oromii* Cobos, 1978 wird zur Gattung *Coptostethus* überstellt; neue Funddaten dieser Art werden mitgeteilt.

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1 Introduction

The Selvage Islands are located approximately 175 km north of the Canary Islands, and almost 290 km south of Madeira (Erber & Weather 1987), and consist of three islands, the Great Salvage, Great Piton, and Piccolo Pitao. Since the very first excursion to the islands, the close relationship between Coleoptera of the Archipelago and those of the Canary Islands has been notorious (Serrano 1983).

Twelve species of *Coptostethus* Wollaston, 1854 are known from the Canary Isles, Madeira and the Selvage Islands, several species are described from the Cape of Good Hope, and one species from North-America.

Cobos (1978) indicated taxonomical similarities between the species of *Coptostethus* living on the Canary Islands and on Madeira, and his newly described *Coptostethus oromii* from the Selvage Islands. At that time, *C. oromii* was the only species of the family Elateridae known from the Selvage Archipelago. Serrano (1983) published data on Coleoptera (Carabidae, Hydraenidae, Staphylinidae, Scymninii, Anobiidae, Ptinidae, Oedemeridae, Mordellidae, Tenebrionidae, Chrysomelidae, and Curculionidae) collected during an expedition to this island. In that paper he did not list any Elateridae, but on page 770 he cited the paper of Cobos (1978) treating *C. oromii* from Great Selvage. Erber & Weather (1987) provided a list of 61 species of Coleoptera from the Selvage Islands, including *Coptostethus oromii* Cobos, 1978.

Recently, in the years 2005, 2006, and 2007, and for the second time at all, specimens of the family Elateridae have been collected from Selvage Islands again. This material consists of *Coptostethus oromii* and two new additional species of the same genus. The new species are described and illustrated in the present paper, the new data on *C. oromii* are recorded.

Holotypes and most paratypes of the new species are preserved in the Museum für Naturkunde Stuttgart (SMNS), some paratypes are stored in the collection of the author (CSV).

Acknowledgements

I would like to express my sincere thanks to Dr. W. Schawaller, Staatliches Museum für Naturkunde (Stuttgart), for providing me with the material for study, and Prof. Dr. D. Putzer (Düsseldorf), for detailed information on his excursions to the Selvage Islands, his kindness in translating the description of *Coptostethus oromii* from Spanish into German, and for his help with special literature. Thanks are also due to Prof. Dr. G. Platia (Gatteo) and an anonymous reviewer who critically read the manuscript.

2 Methods

The body length of the specimens is measured from apical margin of frons to apex of elytra, the body width at level of the middle of the elytra. The antennal length is set in ratio to the combined length of head and pronotum, with the length of the antennomeres as units of measure.

The English expressions for the islands are used in this paper (cf. ERBER & WEATHER 1987).

3 Taxonomy

Coptostethus oromii Cobos, 1978 **n. comb.** (Figs. 1–2)

Cardiophorus (Coptostethus) oromii Cobos, 1978: COBOS (1978: 147–149). Type locality: Selvage Islands: Selvagem Grande (Great Salvage).
Cardiophorus (Coptostethus) oromii Cobos, 1978: SERRANO (1983: 769–770).
Cardiophorus oromii Cobos, 1978: ERBER & WEATHER (1987: 164).

The characteristics of the species classify it to belong to *Coptostethus*. Accordingly it is here transferred to this genus.

New material: Selvage Islands: Selvagem Grande (Great Salvage), north-east of Pico de Inferno, 18.X.2005, 5 specimens (2 CSV, 3 SMNS), leg. D. PUTZER; Selvagem Grande, 5.–20.X.2005, 3 specimens (2 CSV, 1 SMNS), leg. D. PUTZER; same locality but 29.XI.2006, 7 specimens (1 CSV, 6 SMNS), leg. D. PUTZER.

Habitat

The specimens have been found on slightly wet, fine substrate under flat stones.

Coptostethus putzeri **n. sp.** (Figs. 3–10)

Holotype ♂ (SMNS): Selvage Islands: Selvagem Grande (Great Salvage), 5.–20.X.2005, leg. D. PUTZER.
Paratypes 6 ♂♂: Same data as holotype, 3 specimens (2 CSV, 1 SMNS), leg. D. PUTZER; same locality but 29.XI.2006, 3 specimens (SMNS), leg. D. PUTZER.

Etymology

Named in honour of the collector of the new species, Prof. Dr. D. PUTZER, Düsseldorf.

Diagnosis

Elongate, almost three times as long as wide (body length 3.2 mm, body width 1.1 mm); body conspicuously constricted between pronotum and elytra, slightly raised and shiny. Yellow; head, pronotum and a longitudinal strip along suture of elytra reddish-brown. Pubescence yellowish, short and fine, on head and elytra declined to apex, on pronotum declined in various directions.

Description

Head flat; frons almost rectangular and projecting the clypeus, slightly raised above the base of antennae and completely edged; puncture dense and flat, micro-reticulate, just visible, interstices of points half to once their diameter; antennae elongate, surpassing the posterior angles of the pronotum by the last four antennomeres, the latter fusiform, second antennomere little longer than half of the length of third antennomere, last antennomere oval, sub-apically bevelled; antennae covered with short and bristly hairs.

Pronotum sub-globular, its disk a little smaller than that of elytra, along median line slightly longer than wide at middle; pronotum slightly raised, conspicuously arcuate on lateral sides, constricted at the base of posterior angles, the latter pointed backwards and acute at apex; lateral sides of pronotum smooth, without a carina or line; carina of the posterior angles very short and little raised; puncture dense and flat, micro-reticulate, just visible, interstices of points half their diameter; hairs short and bristly, declined in various directions.

Scutellum (Fig. 8) flat, cordiform, convex at base, laterally and apically arcuate; surface flat, puncture micro-reticulate, fine, just visible, interstices of points three to four times their diameter, pubescence fine and short, declined from base to apex.

Elytra sub-oval, little raised and little wider than pronotum, after middle narrowed to apex; apex arcuate, without an inner tooth; base as wide as that of pronotum, regularly edged and triangular, laterally with a conspicuous tooth and forming for the accommodation for the posterior excavations of the pronotum (Fig. 9); shoulder flat (wings reduced); striae of elytra with longitudinal rows of fine and oval, simple puncture, interstices of striae flat, finely micro-punctate and moderately shiny; pubescence short, bristly, declined to apex.

Pro-, meso- and metathorax with fine puncture, interstices of points flat and moderately shiny; pubescence short and fine.

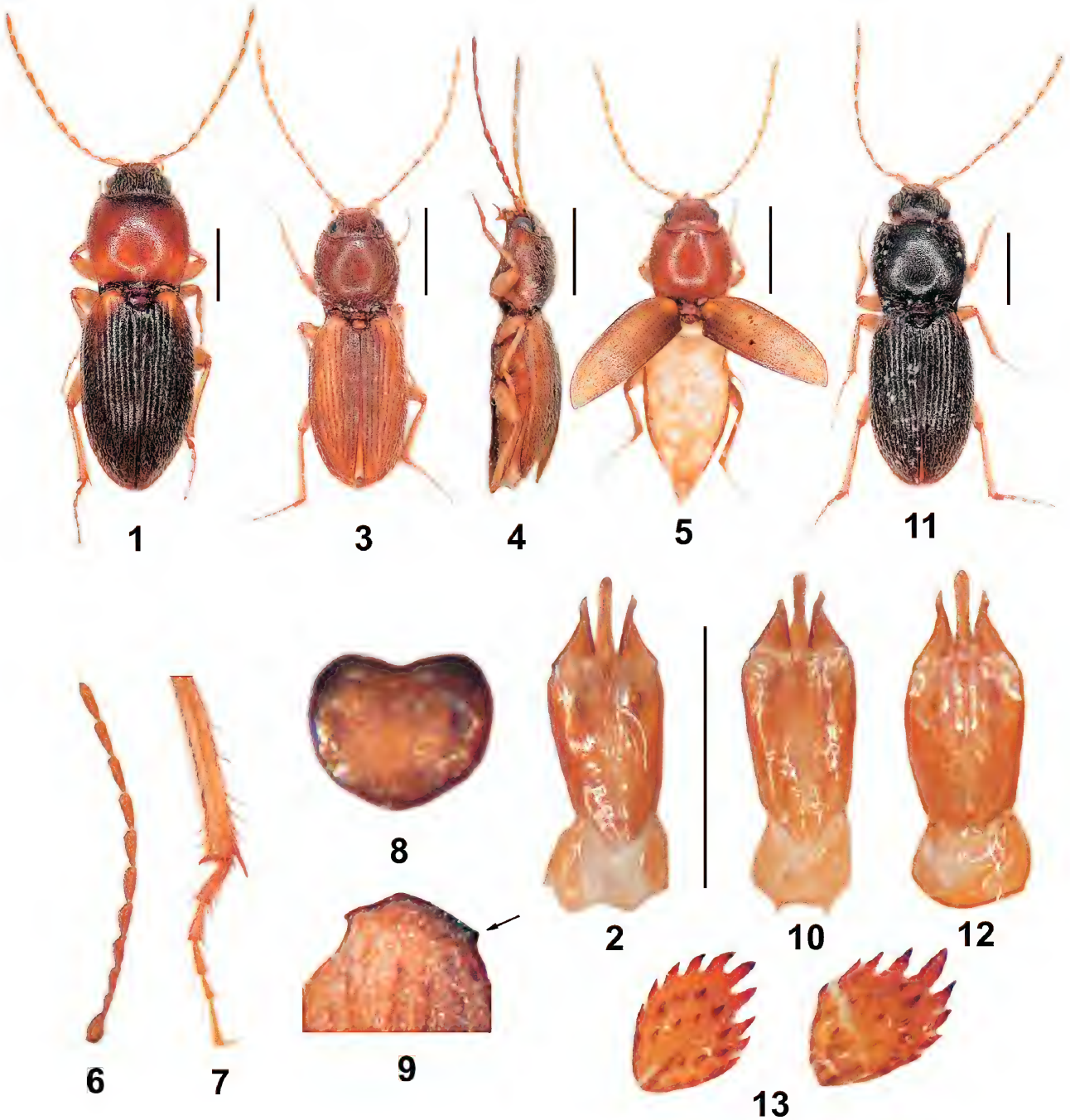
Legs slender, moderately long and thin; femora thickened at apex; lateral sides and apex of tibiae covered with conspicuously extended thorns; tarsus covered with long and fine, apically extended hairs; claws simple; tarsomeres up to claws of decreasing length.

Aedeagus trilobate, with a median lobe just surpassing the apices of the parameres, the latter without lateral edge, just slightly arcuate, and with a long, uncinate bristle at apex.

Female unknown.

Differential diagnosis

The new species, *C. putzeri* n. sp., is closely allied to *C. oromii* Cobos, 1978, but can easily be separated from this species by the smaller body, the lighter colour, the longer antenna (antenna of *C. oromii* surpassing the posterior angles of the pronotum by the last three antennomeres) (Figs. 1, 3–5), and the parallel median lobe of the aedeagus (slightly thickened apically in *C. oromii*) (Figs. 2, 10).



Figs. 1–13. *Coptostethus* spp. – **1–2**. *Coptostethus oromii*. **1** Habitus. **2**. Aedeagus. – **3–10**. *C. putzeri* n. sp. **3**. Habitus, dorsal view. **4**. Habitus, lateral view. **5**. Habitus, open elytra. **6**. Right antenna. **7**. Tibia and tarsus. **8**. Scutellum. **9**. Base of elytra with lateral tooth (arrow). **10**. Aedeagus. – **11–13**. *C. selvagensis* n. sp. **11**. Habitus. **12**. Aedeagus. **13**. Bursa copulatrix. – Scales: 1 mm (1, 3–5, 11), 0.5 mm (2, 10, 12–13).

Variability

The specimens are only slightly variable in their dimensions (body length 3.2–3.6 mm) and characteristics. Two of the paratypes have yellowish heads and pronota.

Habitat

The specimen have been found on slightly wet, fine substrate under flat stones.

Coptostethus selvagensis **n. sp.** (Figs. 11–13)

Holotype ♂ (SMNS): Selvage Islands: Selvagem Grande (Great Salvage), 5.–20.X.2005, leg. D. Putzer.

Paratypes 5 ♂♂, 3 ♀♀: Same data as holotype, 3 specimens (2 CSV, 1 SMNS), leg. D. Putzer; same locality but 29.XI.2006, 5 specimens (SMNS), leg. D. Putzer; Selvagem Grande, north-east of Pico de Inferno, 18.X.2005, 1 specimen (CSV), leg. D. Putzer.

Etymology

Named after the locus typicus.

Diagnosis

Elongate, three times as long as wide (body length 4.2 mm, body width 1.4 mm); body conspicuously constricted between pronotum and elytra, slightly raised, shiny. Chestnut-brown, legs and antennae yellowish, ventral side and basal angles of elytra, as well as disk of scutellum reddish-brown. Pubescence yellowish, short and fine, on head and elytra declined to apex, on pronotum declined in various directions.

Description

Head flat; frons almost rectangular and projecting the clypeus, slightly raised above the base of antennae and completely edged; puncture dense and flat, micro-reticulate, just visible, interstices of points half to once their diameter; antennae elongate, surpassing the posterior angles of the pronotum by the last four antennomeres, the latter fusiform, second antennomere two-thirds of the length of third antennomere, last antennomere oval, subapically bevelled; antennae covered with short and bristly hairs.

Pronotum sub-globular, its disk a little smaller than that of elytra, along median line slightly longer than wide at middle; pronotum slightly raised, conspicuously arcuate on lateral sides, constricted at the base of posterior angles, the latter pointed backwards, and being acute at apex; lateral sides of pronotum smooth, without a carina or line; carina of the posterior angles very short and just little raised; puncture dense and flat, micro-reticulate, just visible, interstices of points half their diameter; hairs short and bristly, declined in various directions.

Scutellum flat, cordiform, convex at base, laterally and apically arcuate; surface flat, puncture micro-reticulate, fine, just visible, interstices of points three to four times their diameter, pubescence fine and short, declined from base to apex.

Elytra sub-oval, little raised and little wider than pronotum, after middle narrowed to apex; apex arcuate, without an inner tooth; base as wide as that of pronotum, regularly edged and triangular, laterally with a conspicuous tooth and forming for the accommodation for the posterior excavations of the pronotum; shoulder flat (wings reduced); striae of elytra with longitudinal rows of fine and oval, simple puncture, interstices of striae flat, finely micro-punctate and moderately shiny; pubescence short, bristly, declined to apex.

Pro-, meso- and metathorax with fine puncture, interstices of points flat and moderately shiny; pubescence short and fine.

Legs slender, moderately long and thin; femora thickened at apex; lateral sides and apex of tibiae covered with conspicuously extended thorns; tarsus covered with long and fine, apically extended hairs; claws simple; tarsomeres up to claws of decreasing length.

Aedeagus trilobate, with a median lobe just surpassing the apices of the parameres, the latter without lateral edge, just slightly arcuate, and with two long, uncinate bristles at apex.

The female has a larger, laterally more arcuate, conspicuously raised body (length/width ratio 5.7 : 2.2). Bursa copulatrix see Fig. 13.

Differential diagnosis

The new species, *C. selvagensis* n. sp., is closely allied to *C. femoratus* Wollaston, 1854 from Madeira, but can easily be separated from the latter by the darker colour of the body and the form of the aedeagus (Fig. 12). The median lobe of *C. femoratus* is conspicuously thin and sharp apically, see Cobos (1978).

Variability

The specimens are only slightly variable in their dimensions (body length of males 3.7–4.3 mm, of females 5.7–6.0 mm), characteristics and colour.

Habitat

The specimens have been found on slightly wet, fine substrate under flat stones.

4 Discussion

The absence of wings is a reductive characteristic of all species of the genus, as well as in other Elateridae living on small islands like the Selvages. This is a quite interesting fact, as the next relatives of *Coptostethus*, the species of the genus *Cardiophorus*, which are living on the continent, possess intact wings and flying muscles, and move mostly by flying. The evolutionary benefit for *Cardiophorus* and *Coptostethus*, either with or without wings seems to be strictly dependent of the place where the species live, either on the continent or on a small island. Within the Elateridae this characteristic is often discussed as convergence, as the reduction of wings in various groups undoubtedly has been evolved independently.

The constriction between pronotum and elytra in the

species of *Coptostethus* is very probably based on a functional necessity too. As the species of the genus *Coptostethus* have lost their wings, they move exclusively with their legs. Therefore, this constriction undoubtedly has to be interpreted as a reduction to accommodate the knees of the fore and middle legs while moving. In most of the species of the genus *Cardiophorus* the pronotal and elytral bases are wider, and the space between these parts is only slightly constricted. It seems, that there is no need for these species to have open space between the pronotal and elytral bases to accommodate the knees while moving. Hence, the constriction between pronotal and elytral bases in *Coptostethus* is connected with the reduction of the wings.

The triangular base of the elytra, which possess a conspicuous tooth at the lateral end, fits perfectly into the opposite excavation of the pronotal base, and may present a functional characteristic too. The tooth and the edged base undoubtedly stabilize the pronotum while the specimen is preparing for jumping. The constitution of the base of the elytra of *Coptostethus* together with the excavation of the pronotal base represent a part of the mechanism, which includes primary the prosternal apophysis and the mesosternal cavity for the jumping behaviour.

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Manuscript received: 1.VI.2007, accepted: 14.VIII.2007.

Revision of the genus *Pseudethas* Fairmaire, with descriptions of four new species from Nepal and Thailand (Coleoptera: Tenebrionidae: Stenosini)

René Fouquè

Abstract

The species of the genus *Pseudethas* Fairmaire, 1896 (Coleoptera: Tenebrionidae: Stenosini) are revised, and four new species are described. Diagnostic characters are illustrated. A key to all species is provided. – New species: *Pseudethas (Pseudethas) longigenus* **n. sp.** (Nepal), *P. (P.) schawalleri* **n. sp.** (Nepal), *P. (P.) thailandicus* **n. sp.** (Thailand), *P. (Stenillus) weigeli* **n. sp.** (Nepal).

Keywords: Coleoptera, Tenebrionidae, Stenosini, *Pseudethas*, new species, Nepal, Thailand, aedeagus.

Zusammenfassung

Die Arten der Gattung *Pseudethas* Fairmaire, 1896 (Coleoptera: Tenebrionidae: Stenosini) werden revidiert mit Beschreibungen von vier neuen Arten. Die diagnostischen Merkmale werden abgebildet. Ein Bestimmungsschlüssel für alle Arten wird aufgestellt. – Neue Arten: *Pseudethas (Pseudethas) longigenus* **n. sp.** (Nepal), *Pseudethas (P.) schawalleri* **n. sp.** (Nepal), *Pseudethas (P.) thailandicus* **n. sp.** (Thailand), *P. (Stenillus) weigeli* **n. sp.** (Nepal).

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1 Introduction

The genus *Pseudethas* Fairmaire, 1896 (including the newly described four species of the present paper) consists of 15 species in two subgenera. Its type species is *Pseudethas quadraticeps* Fairmaire, 1896, described from Simla (India, Uttaranchal). *P. rogersi* (Wasmann, 1899) was described in the new genus *Schizillus* from Mussoorie (India-Uttar Pradesh), but since this genus name was a homonym of *Schizillus* Horn, 1874, Wasmann (1902) erected the replacement name *Dischizillus*. Blair (1927) described the monotypic new genus *Stenillus* from Tibet (*S. monticola*), and he also indicated that *Dischizillus* was synonymous with *Pseudethas*. Kaszab (1960) described *P. afghanicus* from Afghanistan and attached a first key to three species of the genus. The genus *Stenillus* was downgraded by Kaszab (1973) to a subgenus of the genus *Pseudethas*. later, Kaszab (in Kaszab et al. 1978) described a new subspecies, *P. rogersi ladakhensis*, from Ladakh. The number of species was growing to ten, when Kaszab (1981) upgraded the subspecies *ladakhensis* to species level and described five additional new species (*P. antennalis*, *P. nepalicus*, *P. costatus*, *P. pakistanus* and *P. incostatus*) from Nepal, Pakistan and India. This study also contained a key to species and photographs of the newly described species. Finally, Schawaller (2001) described *P. jaegeri* from Tibet with drawings of the dorsal view, part of the legs and the aedeagus. A checklist of the known species of *Pseudethas* is added in this paper.

Medvedev (1994) indicated in his key to genera and subgenera of the tribe Stenosini that the pronotum of the subgenus *Stenillus* is "without medial depression or flatted area". However, this is not always true because the pronotum of *P. (Stenillus) monticola* (Blair, 1927) shows a distinct flattened area medially in its posterior third.

Type material of all species except *P. quadraticeps* Fairmaire, 1896 was available to me. Blair's label "Type" and Wasmann's label "Cotype" are here interpreted as holotype and paratype, respectively. Specimens of the genus *Pseudethas* are rare in collections, probably due to the small body size and the small remote distribution areas.

Species of the genus *Pseudethas* are distributed at altitudes between 1300–5150 m from the Hindu Kush in Afghanistan, over Karakoram, northern India, east Himalaya up to Mount Everest, but a newly described species is now surprisingly also known from the Thai province Phetcha

Buri (situated at the base of the Malayan peninsula) at an altitude of only 40 m (Fig. 1). This is the first record of *Pseudethas* from Southeast Asia and also a new tenebrionid genus for the Thai fauna. Only the genera *Stenosis*, *Dichillus* and *Gebieniella* were hitherto known from Thailand. The locality Ban Sa Yai Non, where I collected together with my colleague STANISLAV BEČVÁŘ, is situated in coastal lowland and shows steppe character (Fig. 60).

WASMANN (1899) mentioned that *P. rogersi* had been collected in nests of the ant *Pheidole indica* Mayr 1879. *P. afghanicus* Kaszab, 1960 was collected under stones in ants' nests of the genus *Tapinosoma* (KASZAB 1960). *P. ladakhensis* was found under stones in irrigation channels (KASZAB et al. 1978), and SCHAWALLER (2001) stated, that *P. jaegeri* was also collected under stones. *P. thailandicus* n. sp. was found by me under stones as well, but also under a piece of wood and under a fallen abandoned ant-nest of the genus *Crematogaster*.

The genus *Pseudethas* is characterized by parallel elytra and a flattened surface. The elytral base is considerably wider than the pronotal base. The tempora are often convex, sometimes just parallel. The pronotum usually has a median longitudinal impression, which may be only very slightly developed at times. Males possess a small tooth each on the inner side of the middle and posterior tibiae. Body length is between 2.7 and 4.8 mm.

Herbertfranzia Kaszab, 1973, a closely related genus with a single endemic species in Nepal, can be distinguished by its oval elytra, arched body, elytral base hardly wider than pronotal base, and pronotum without impression.

KASZAB (1981) stated that *P. costatus* eventually has to be transferred into a new subgenus or even genus. He mentioned that this species is more similar to *Indochillus* than to *Pseudethas*: "Diese Art weicht von allen bekannten Arten der Gattung *Pseudethas* wesentlich ab. Charakteristisch sind die vier Flügendeckenrippen sowie der in der Mitte nicht eingedrückte Halsschild.". This is not quite correct, however, because there is a very faint impression on the posterior third of the pronotum. I classify this species in the genus *Pseudethas (Pseudethas)* because it has all generic characters of *Pseudethas*.

The genus *Indochillus* Koch, 1941, described from India, is similar to *Pseudethas* but is distinguished by the following characters: base of pronotum of same width as elytral base, elytra gradually extending from base, temporae very long, gradually converging and with abrupt cervical constriction, keels on inner side of eyes prominent. The genus *Indochillus* is in need of revision, and especially the position of the newly described species *I. convexigena* Ren & Shi (see REN & SHI 2006) needs to be established.

Abbreviations of museums and collections

CBS	Collection STANISLAV BEČVÁŘ, České Budějovice, Czech Republic
CFR	Collection RENÉ FOUQUÈ, Liberec, Czech Republic
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Dr. OTTÓ MERKL)
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland (Dr. GIULIO CUCCODORO)
NHM	The Natural History Museum, London, U. K. (MAX BARCLAY)
NHMB	Naturhistorisches Museum, Basel, Switzerland (Dr. MICHEL BRANCUCCI, ISABELLE ZÜRCHER)
NHMB-F	Naturhistorisches Museum, Basel, Switzerland, collection FREY (Dr. EVA SPRECHER)
NKME	Naturkundemuseum, Erfurt, Germany (MATTHIAS HARTMANN)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (Dr. WOLFGANG SCHAWALLER)

Acknowledgements

I would like to thank all curators and colleagues for the loan of material. Special thanks go to Dr. WOLFGANG SCHAWALLER (SMNS) for his help. This work is dedicated to my old friend STANISLAV BEČVÁŘ (České Budějovice), for his help and inspiration not only on expeditions. Thanks are also due to my colleagues LUBOŠ DEMBICKÝ (Moravian Museum, Brno) for preparing the photographs and FABRIZIO RIGATO (Museo Civico di Storia Naturale, Milano) for the determination of the ant genus *Crematogaster* based on a photograph of the nest.

2 Methods

The length of the head is measured from the front margin of the clypeus to the cervical constriction. The length of the elytra is measured from anterior corner to apex.

In the lists of materials, some localities are not cited in the original spelling of the labels, but are given in a standardized form. The former Indian state Uttar Pradesh (U. P.) was divided into Uttar Pradesh and the new state Uttaranchal in November 2000; this new situation is considered in the present paper.

3 The previously known species of *Pseudethas*

Pseudethas (Pseudethas) afghanicus Kaszab, 1960 (Figs. 11, 42–44)

Pseudethas afghanicus Kaszab, 1960 – KASZAB 1960: 3.

Studied type material: E Afghanistan, Hindu Kush (Hindukusch), Salang Valley, Walang, 2550 m, 14.XI.1952, leg. J. KLAPPERICH, 2 ♂♂, 3 ♀♀ paratypes HNHM, 2 ♂♂, 2 ♀♀ paratypes NHMB-F, 1 ♀ paratype NHM.

New material: None.

Distribution: Afghanistan (Hindu Kush).

Remarks: A species with notably parallel tempora which are as long as the eye. KASZAB (1970) mentions additional localities in Afghanistan: Bag-Chah Babar (Kabul), Tchidjan (close to Cheikhabad), Kouh-Ghar Khvadjah (close to Mazanah, Ghorband Valley).

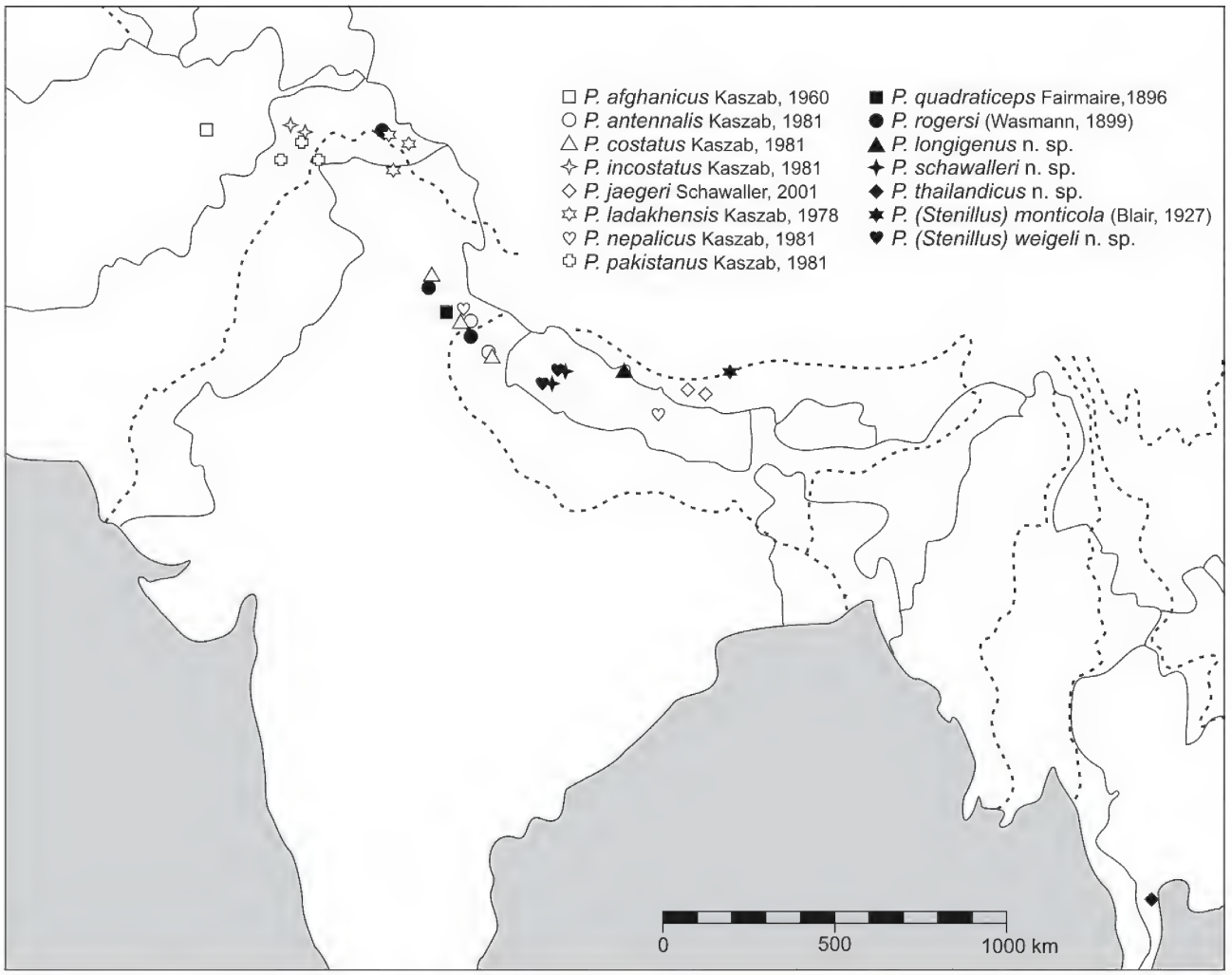


Fig. 1. Distribution of *Pseudethas* spp.

Pseudethas (Pseudethas) antennalis Kaszab, 1981 (Figs. 7, 30–32)

Pseudethas antennalis Kaszab, 1981 – Kaszab 1981: 298.

Studied type material: India, Uttaranchal (labelled U. P.), Kumaon, W Almora Divn., January 1919, leg. H. G. Champion, ♀ holotype HNHM. – India, Uttaranchal (labelled U. P.), Ranikhet, June–August 1916, leg. H. G. Champion, 1 ♀ paratype HNHM.

New material: Same data as holotype, 2 ♀♀ NHM. – Same data as paratype, 3 ♀♀ NHM. – India, Uttaranchal (labelled U. P.), Nainital, 1900 m, 27.VI.1989, leg. R. Schuh, 1 ♀ CBS. – India, Uttaranchal, Nainital env., 1900–2100 m, 19.–21. VI.2003, leg. Z. Kejval & M. Trýzna, 1 ♂ CFR. – N India, Uttaranchal state, 30 km N of Rishikesh, NW of Chamba, Arakot vill. env, 1500 m, 29.–31.VII.2003, leg. Z. Kejval & M. Trýzna, 1 ♀ CFR.

Distribution: India (Uttaranchal).

Remarks: A robust species, distinguished from other *Pseudethas* by the longitudinal pronotal impression over its whole length, the extraordinary thick antennae and the notably parallel elytra. In the NHM collection this species was erroneously determined as *P. rogersi*, which is superficially similar, but can be distinguished by the apically widened antennae and rounded elytra. The aedeagus of the only available male (body length 3.8 mm) of *P. antennalis* is figured in this paper (Fig. 32).

Pseudethas (Pseudethas) costatus Kaszab, 1981 (Figs. 12, 45–47)

Pseudethas costatus Kaszab, 1981 – Kaszab 1981: 303.

Studied type material: India, Uttaranchal, Nainital, 8400 ft. (2560 m), 14.II.1934, leg. J. A. Graham, 1 ♂ paratype NHM. – India, Uttaranchal (labelled U. P.), Chakrata, VI.1923, leg. C. F. C. Beeson, 1 ♀ paratype NHM. – India, Uttaranchal (labelled U. P.), Mundali, Chakrata, 11.IV.1933, leg. J. C. M. Gardner, 1 ♀ paratype NHM. – India, Uttaranchal (la-

belled U. P.), Mundali 8408 (2560 m), Chakrata, 29.V.1937, leg. J. C. M. GARDNER (ex *Quercus dilatata*), 1 ♂ paratype HNHM. – India, Uttaranchal (labelled U. P.), Deoban, 9700 ft. (2960 m), Chakrata, 21.VI.1933, leg. B. M. BHATIA (under stone), 1 ♀ paratype HNHM.

New material: India, Himachal Pradesh, Kulu, 7000 ft. (2130 m), NHMB-F – erroneously identified by REITTER as *P. rogersi*.

Distribution: India (Uttaranchal, Himachal Pradesh).

Remarks: *P. costatus* is a large species, remarkable because of its strongly roof-shaped keels of the 3rd, 5th, 7th and 9th elytral intervals and prominent humeral corners. KASZAB (1981) also mentioned that this species had no impression in the middle of the pronotum, but a weak impression is found in its posterior third. *P. schawalleri* n. sp. is similar to this species, distinguished by its slightly convex non-keeled elytral intervals (which are flat in *P. costatus*), and different shape of pronotum and head.

Pseudethas (Pseudethas) incostatus Kaszab, 1981 (Figs. 15, 54–56)

Pseudethas incostatus Kaszab, 1981 – KASZAB 1981: 302.

Studied type material: Pakistan, Kalam, Swat, 6830 ft. (2080 m), ♀ holotype HNHM.

New material: Pakistan, Swat, Vallée d'Ushu, 2300 m, 15.V.1983, leg. BESUCHET & LÖBL, 46 ex. MHNG, 3 ex. SMNS, 2 ex. CBS. – Pakistan, Swat, Kalam, 2100 m, 12.V.1983, leg. BESUCHET & LÖBL, 1 ex. MHNG. – Pakistan, Swat, s/Utrot, 2500–2600 m, 13.V.1983, leg. BESUCHET & LÖBL, 2 ex. MHNG. – Pakistan, Chitral, Lawarai Pass, 2600 m, 23.V.1983, leg. BESUCHET & LÖBL, 8 ex. MHNG, 1 ex. SMNS, 1 ex. CBS. – Pakistan, Chitral, Bumburet, 2200–2350 m, 24.V.1983, leg. BESUCHET & LÖBL, 11 ex. MHNG, 1 ex. SMNS, 2 ex. CBS. – Pakistan, Chitral, s/Madaglasht, 2900–3050 m, 27.V.1983, leg. BESUCHET & LÖBL, 1 ex. MHNG. – Pakistan, Chitral, Kalas, 1900 m, 28.V.1983, leg. BESUCHET & LÖBL, 2 ex. MHNG. – Pakistan, Chitral, Lotkoh, 2350 m, 29.V.1983, leg. BESUCHET & LÖBL, 1 ex. MHNG.

Distribution: Pakistan (North West Frontier Province).

Remarks: The holotype is a female; therefore the aedeagus pictured in this paper is taken from a non-type specimen. This species is most numerous in collections; besides the holotype 82 specimens were collected during an expedition of C. BESUCHET and I. LÖBL (Genève). *P. pakistanus* is very similar, mainly distinguished from *P. incostatus* by the shape of its head and pronotum.

Pseudethas (Pseudethas) jaegeri Schawaller, 2001 (Figs. 14, 51–53)

Pseudethas jaegeri Schawaller, 2001 – SCHAWALLER 2001: 143.

Studied type material: Tibet, 44 km SW Tingri, La-Lung La (Tong La), N28°30'59.9, E86°10'2.1, 5150 m, 5.VIII.1998, leg. O. JÄGER, 1 ♂ paratype SMNS.

New material: SW Tibet, Himalaya Mts., 60 km south of Saga, 4600–5000 m, 23.–24.VI.2004, leg. V. MAJOR, 2 ♂♂, 1 ♀ CFR.

Distribution: Tibet.

Remarks: Typical for this species are the flattened elytral intervals and the glossy deep black body (including legs and antennae).

Pseudethas (Pseudethas) ladakhensis Kaszab, 1978 (Figs. 9, 36–38)

Pseudethas rogersi ladakhensis Kaszab, 1978 – KASZAB in KASZAB et al. 1978: 223.
Pseudethas ladakhensis – KASZAB 1981: 296.

Studied type material: India, Ladakh, Kargil, 2950 m, 30.V.–7.VI.1976, leg. MARTENS & SCHAWALLER, 1 ♂ paratype HNHM.

New material: Pakistan, Alchori, Valle Shigar, 26.IV.1929, 1 ex. NHMB-F. – Pakistan, Baltistan Prov., Hushe Valley, 5 km south from Hushe, 2800 m, 28.VIII.1997, leg. M. ŠLACHTA (under stone), 1 ♀ CBS. – Pakistan, Karakoram Mts., Baltistan Prov., Hushe Valley, 3 km N of Kande, 3070 m, 17.IX.2001, leg. M. ŠLACHTA, 4 ♀♀ CBS.

Distribution: India (Jammu and Kashmir), Pakistan (Northern Areas).

Remarks: *P. ladakhensis*, superficially similar to *P. rogersi*, differs mostly in the shape of the head (tempora gradually narrowing towards cervix and genae not extended, widest at level of eyes).

Pseudethas (Pseudethas) nepalicus Kaszab, 1981 (Figs. 5, 24–26)

Pseudethas nepalicus Kaszab, 1981 – KASZAB 1981: 299.

Studied type material: Nepal, Kathmandu Valley, Balaju, 1300–1370 m, 23.V.1977, leg. WITTMER & BRANCUCCI, ♂ holotype NHMB.

New material: Same data as holotype, 4 ex. NHMB. – India, Himachal Pradesh, Chopal-Khangna Nallah, 2000–2300 m, 7.V.1977, leg. WITTMER & BRANCUCCI, 2 ♂♂, 1 ♀ HNHM. – India, Himachal Pradesh, Chopal, 2400–2750 m, 7.V.1977, leg. WITTMER & BRANCUCCI, 1 ♂ HNHM. – India, Himachal Pradesh, Simla, Tharoch, 6500 ft. (1980 m), 22.V.1924, leg. B. M. BHATIA (under stone), 1 ♀ HNHM.

Distribution: Nepal (Kathmandu Valley), India (Himachal Pradesh).

Remarks: There are four specimens in NHMB with the same label data as the holotype, but they were obviously not included in the type series by KASZAB. Another specimens in NHMB and HNHM were erroneously identified as *P. quadraticeps* and *P. rogersi*, distinguished from *P. nepalicus* by number and size of the elytral punctures and the keel of the 7th elytral interval.

Pseudethas (Pseudethas) pakistanus Kaszab, 1981 (Figs. 16, 57–59)

Pseudethas pakistanus Kaszab, 1981 – KASZAB 1981: 301.

Studied type material: Pakistan, Naran, Khagan, 2370–2750 m, 22.VI.1977, leg. WITTMER & BRANCUCCI, ♂ holotype NHMB, 5 ♂♂, 4 ♀♀ paratypes NHMB, 2 ♂♂ HNHM. – Pakistan, Shogran, Khagan, 2300–2750 m, 17.VI.1977, leg. WITTMER & BRANCUCCI, 1 ♀ paratype HNHM.

New material: Pakistan, Swat, Marghuzar, 1300 m, 8.V.1983, leg. BESUCHET & LÖBL, 4 ♂♂ MHNG. – Pakistan, Hazara, s/Naran, 2600 m, 1.VI.1983, leg. BESUCHET & LÖBL, 1 ♀ MHNG. – Pakistan, Hazara, Kaghan, 2150 m, 2.VI.1983, leg. BESUCHET & LÖBL, 1 ♂ SMNS. – Pakistan, Hazara, Shogran, 2400 m, 3.VI.1983, leg. BESUCHET & LÖBL, 2 ♀♀ MHNG. – Pakistan, Hazara, Malkandi, 1500 m, 3.VI.1983, leg. BESUCHET & LÖBL, 1 ♀ MHNG.

Distribution: Pakistan (North West Frontier Province).

Remarks: I know only the type material of KASZAB and specimens from the expedition of BESUCHET and LÖBL. *P. pakistanus* is the smallest species of the genus, similar to *P. incostatus*.

Pseudethas (Pseudethas) quadraticeps Fairmaire, 1896 (Figs. 4, 22–23)

Pseudethas quadraticeps Fairmaire, 1896 – FAIRMAIRE 1896: 57.

Studied type material: None.

New material: India, Himachal Pradesh, Punjab, Simla, Kotkhai, Kalala F., 8000 ft. (2440 m), 14.–15.V.1924, leg. C. F. C. BEESON, 1 ♀ NHM. – India, Himalaya, Himachal Pradesh, Simla, 2 ex. NHMB-F, 2 ex. HNHM.

Distribution: India (Himachal Pradesh).

Remarks: Remarkable because of the distinct keels of the 3rd, 5th, 7th and 9th elytral intervals. Only historical material of this species was available for study.

Pseudethas (Pseudethas) rogersi (Wasmann, 1899) (Figs. 8, 33–35)

Schizillus Rogersi Wasmann, 1899 – WASMANN 1899: 166.
Dischizillus Rogersi – WASMANN 1902: 244.

Studied type material: India, Uttaranchal, Mussoorie, leg. C. ROGERS, 1 ♂ paratype (labelled cotype) HNHM.

New material: India, Uttaranchal, Mussoorie, 6500 ft. (1980 m), July 1924, leg. J. C. M. GARDNER, 1 ♀ NHM. – India, Uttaranchal, Dehra Dun, 2 ex. NHMB-F. – India, Dhelu, Mandi, Punjab, 4500 ft. (1370 m), leg. H. G. CHAMPION, 1 ♂ NHM. – Pakistan, Karakoram, Dusso, 28.IV.1929, 1 ♂ NHMB-F.

Distribution: India (Uttaranchal), Pakistan (Northern Areas).

Remarks: *P. rogersi* has often been confused with other species of *Pseudethas*, so hitherto it seemed to be more common as it is in reality. I saw only historical material from northern India, and one specimen from Dusso in Pakistan, which is situated between Nanga Parbat and K2.

Pseudethas (Stenillus) monticola (Blair, 1927) (Figs. 2, 17–18)

Stenillus monticola Blair, 1927 – BLAIR 1927: 245.
Pseudethas (Stenillus) monticola – KASZAB 1973: 28.

Studied type material: Tibet, Chusar, 13500 ft. (4100 m), 3.V.1924, leg. Maj. R. W. G. HINGSTON, Everest Exp. Brit. Mus. 1924, ♀ holotype (labelled type) NHM.

New material: None.

Distribution: Tibet.

Remarks: Known only from the holotype, which was collected during the third British Mount Everest expedition in 1924.

4 New species of *Pseudethas*

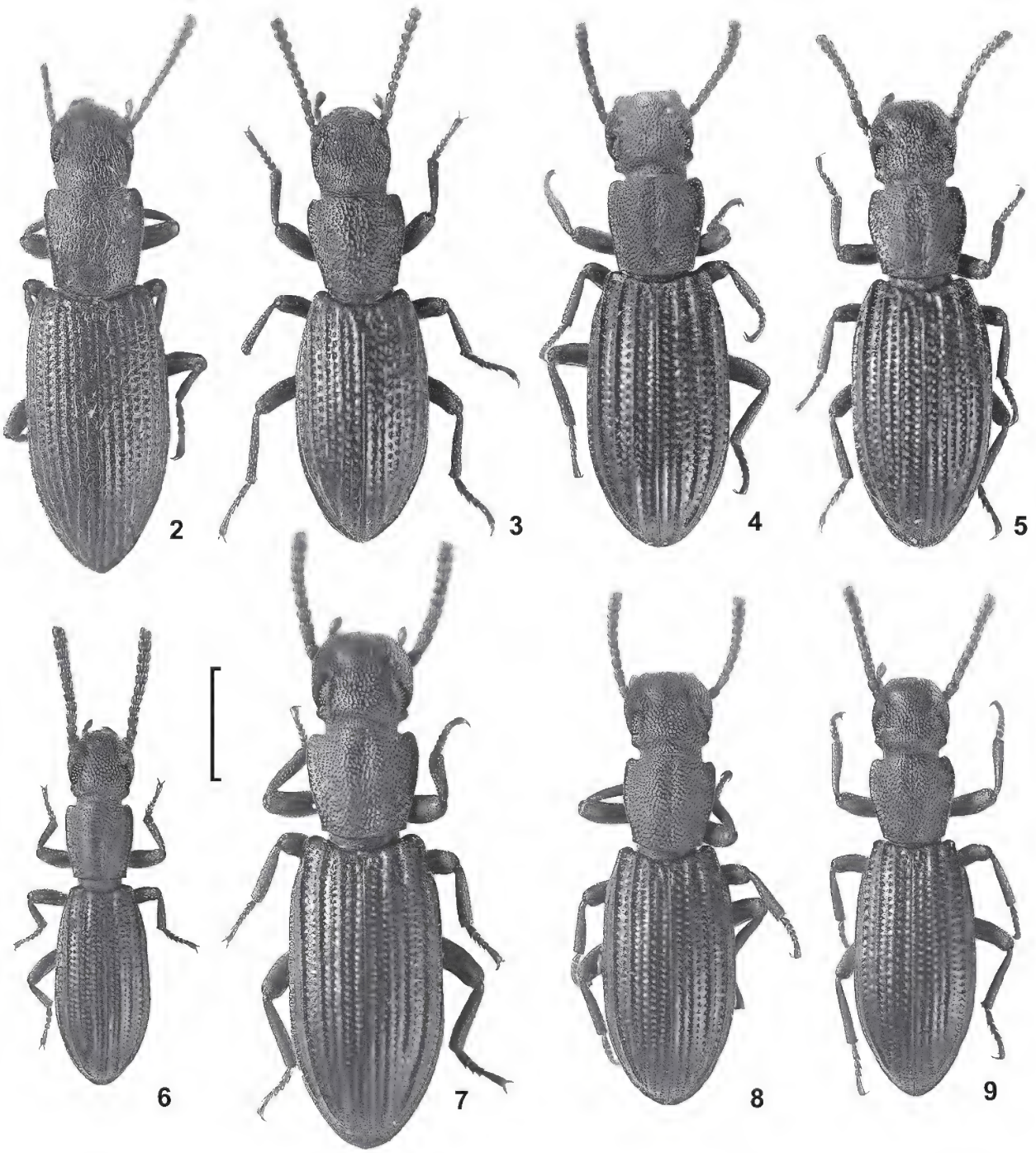
Pseudethas (Pseudethas) longigenus **n. sp.** (Figs. 10, 39–41)

Holotype (♂): Nepal, Mustang District, Kagbeni, Kali Gandaki Valley, 2900 m, 9.VI.1993, leg. D. AHRENS, SMNS.

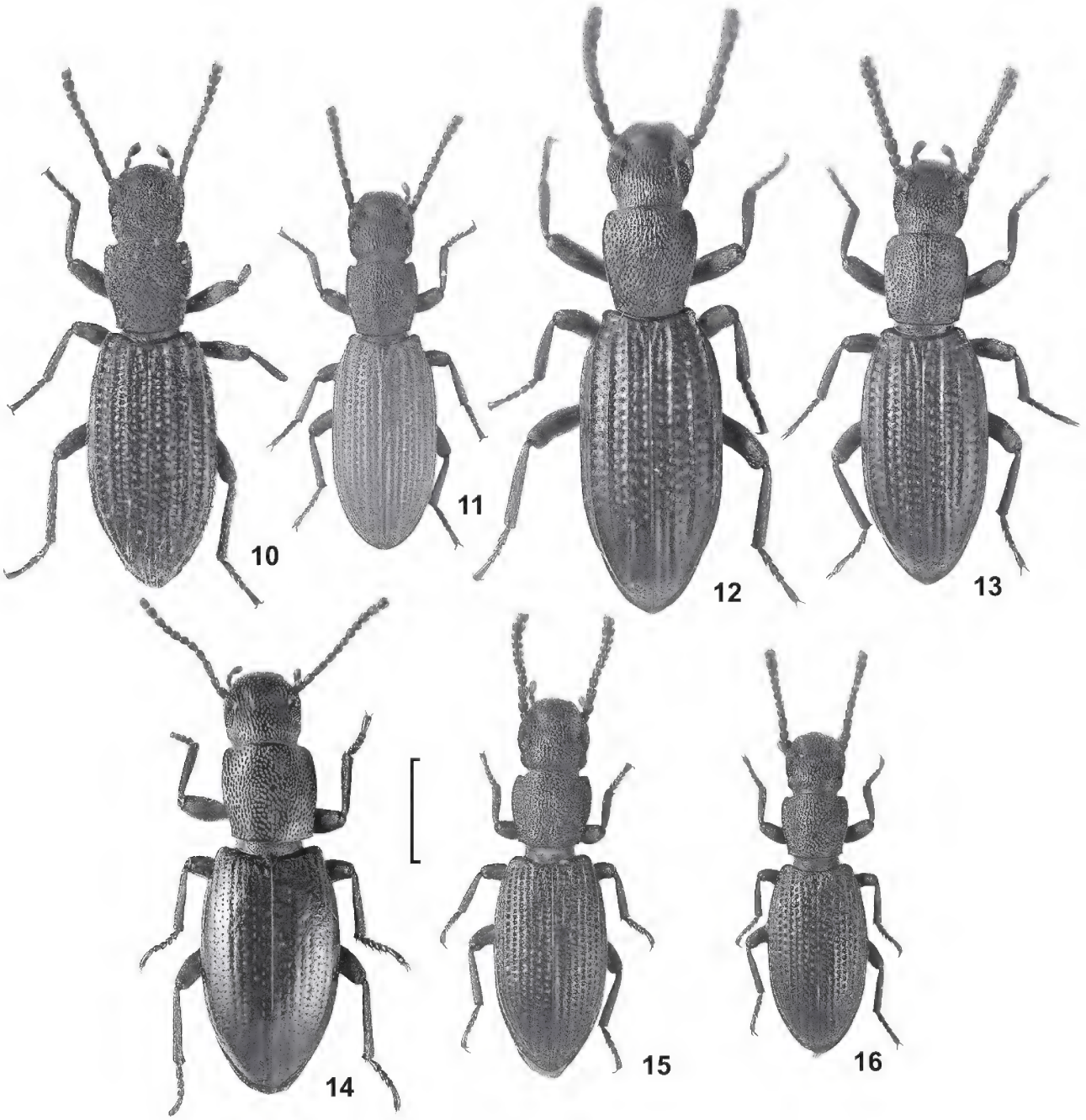
Paratype: Same data as holotype, 1 ♂ SMNS.

Etymology: Named after the characteristic shape of the genae.

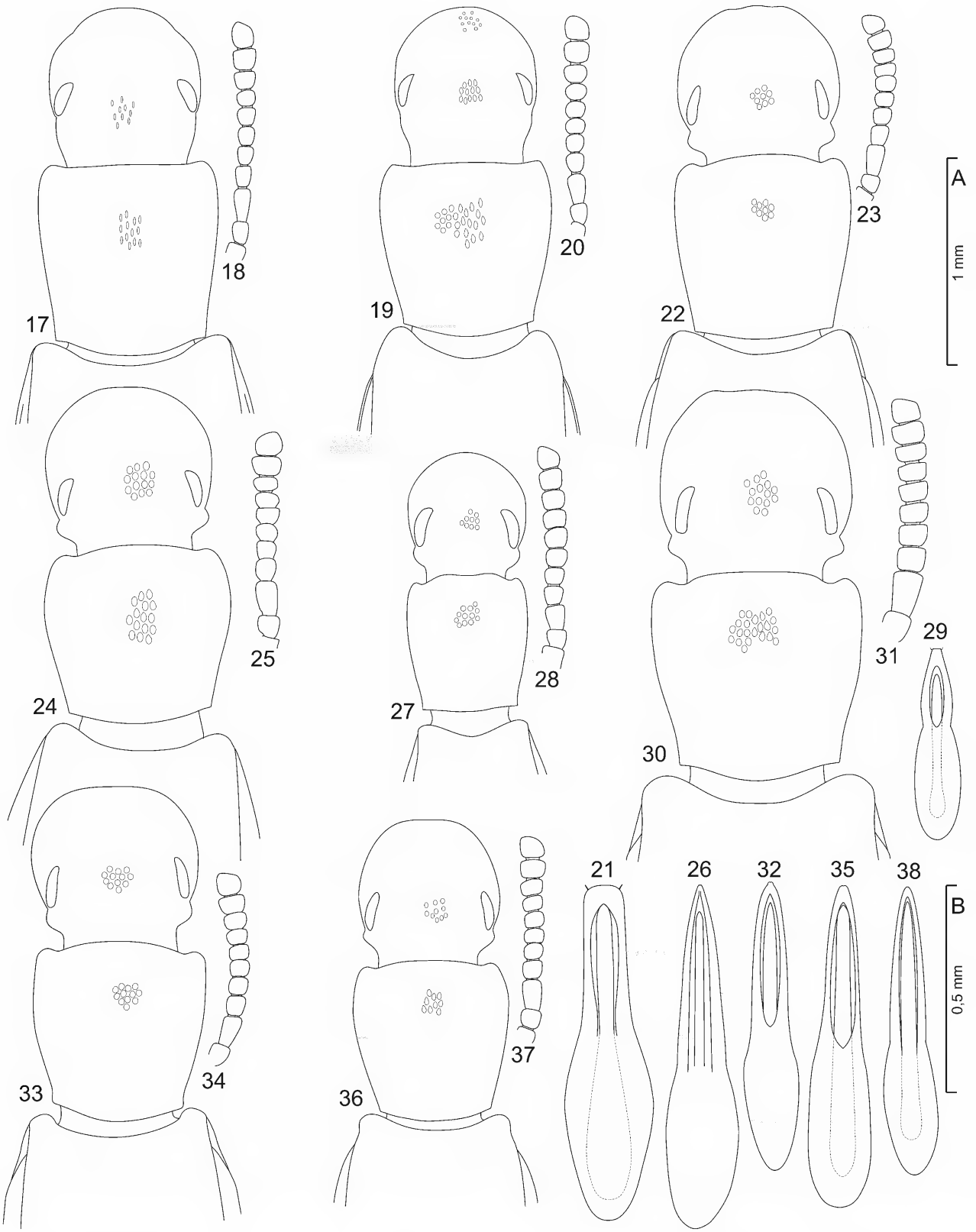
Description: Body length 4.0 mm, body width 1.18 mm. – Body dark-brown, legs and antennae somewhat brighter, 9th–11th antennal segments as dark as body. Body haired with yellow setae. Setae thicker, erect and curved on 5th, 7th, and 9th keel of elytra, as well as on margins of head and pronotum. – Head (Fig. 39): Ratio length/width 51 : 50, widest before eyes. Eyes completely divided by cheeks, dorsal side of eye with about 14 facets in three rows, ventral side with about 9 facets. Tempora almost parallel or only very slightly extending behind the eye over a distance of about one eye length, then gradually narrowing towards the cervical constriction. Genae extending from the posterior margins of the eyes in a gentle arch, and then leading almost straight to the widest part of the head. Clypeus almost straight, slightly convex. Frons with two impressions. Punctulation on vertex rough, punctures on forehead half as large as on vertex; surface between punctures very roughly wrinkled. Antennae (Fig. 40) long-haired; combined 2nd–11th segments twice as long as width of cervix; ratio of lengths of 2nd–11th segments: 7 : 10.8 : 7.3 : 6.3 : 6 : 5.6 : 5.8 : 6 : 7 : 8.1, ratio of widths: 4.4 : 5.1 : 5 : 4.7 : 4.7 : 5 : 5.5 : 6 : 7.2 : 6.5; last segment concave apically. – Pronotum (Fig. 39) wider than head (58 : 50), widest at anterior quarter; ratio length/width 61 : 58, ratio widths at posterior edges/at widest point/at anterior edges 43 : 58 : 49. Anterior corners rectangular, slightly protruding. Posterior corners obtuse. Lateral margin of pronotum nodulated all over its length; nodulation more distinct at first third; one row of thick, curved yellow setae on margin. Punctures on pronotum larger than on head, nearly confluent; surface between punctures very roughly wrinkled. – Elytra: 2.8 times as long, 1.4 times as



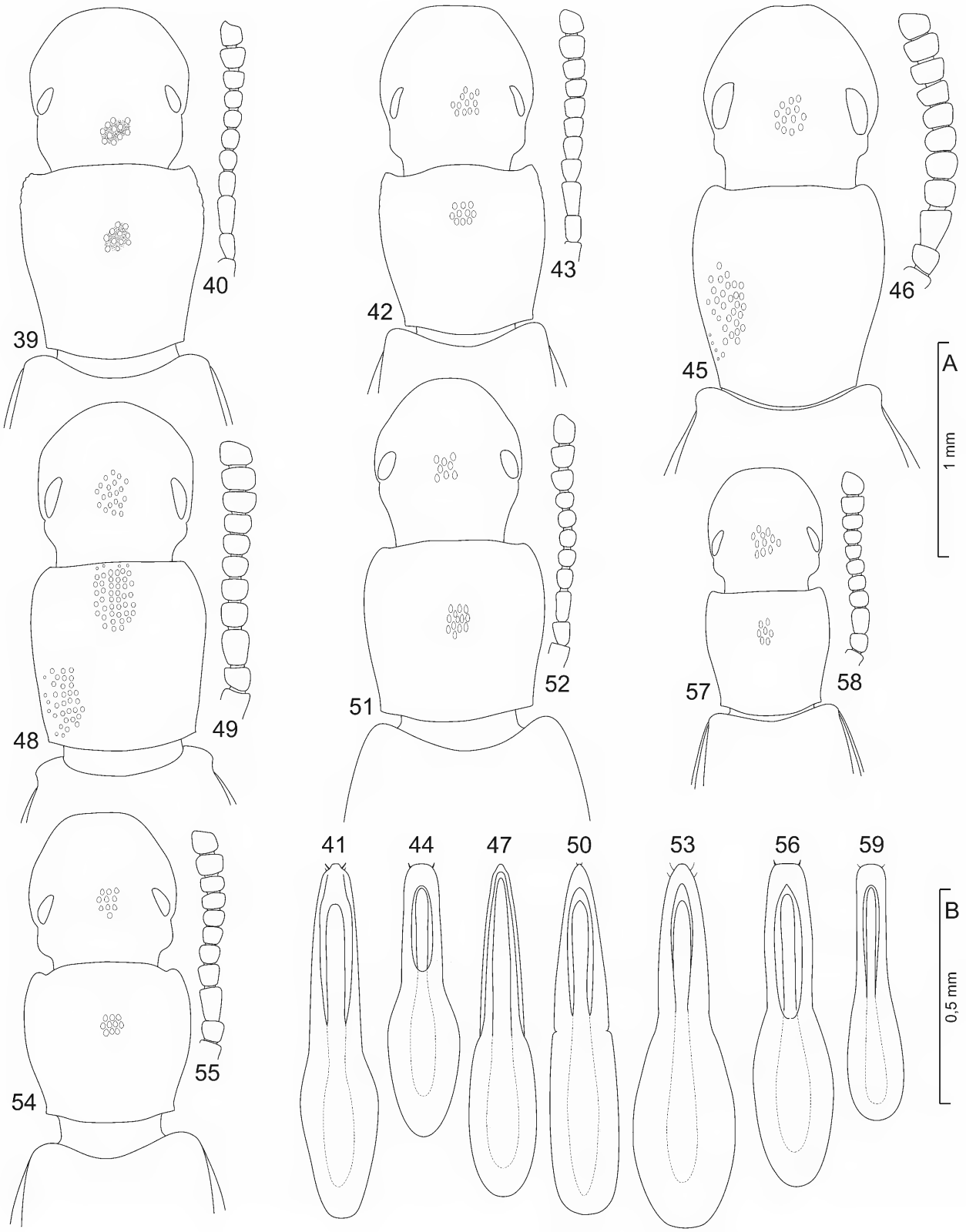
Figs. 2–9. *Pseudethas* spp., dorsal view. – **2**. *P. (Stenillus) monticola*, holotype ♀, Tibet. **3**. *P. (Stenillus) weigeli* n. sp., holotype ♂, Nepal. **4**. *P. (P.) quadraticeps*, ♀, India (Himachal Pradesh). **5**. *P. (P.) nepalicus*, holotype ♂, Nepal. **6**. *P. (P.) thailandicus* n. sp., holotype ♂, Thailand. **7**. *P. (P.) antennalis*, holotype ♀, India (Uttaranchal). **8**. *P. (P.) rogersi*, paratype ♂, India (Uttaranchal). **9**. *P. (P.) ladakhensis*, paratype ♂, India (Ladakh). – Scale: 1 mm.



Figs. 10–16. *Pseudethas* spp., dorsal view. – **10**. *P. (P.) longigenus* n. sp., holotype ♂, Nepal. **11**. *P. (P.) afghanicus*, paratype ♂, Afghanistan. **12**. *P. (P.) costatus*, paratype ♂, India (Uttaranchal). **13**. *P. (P.) schawalleri* n. sp., holotype ♂, Nepal. **14**. *P. (P.) jaegeri*, ♂, Tibet. **15**. *P. (P.) incostatus*, holotype ♀, Pakistan. **16**. *P. (P.) pakistanus*, paratype ♂, Pakistan. – Scale: 1 mm.



Figs. 17–38. *Pseudethas* spp., head, pronotum and elytral base, antenna, aedeagus. – **17–18**. *P. (Stenillus) monticola*. **19–21**. *P. (Stenillus) weigeli* n. sp. **22–23**. *P. (P.) quadraticeps*. **24–26**. *P. (P.) nepalicus*. **27–29**. *P. (P.) thailandicus* n. sp. **30–32**. *P. (P.) antennalis*. **33–35**. *P. (P.) rogersi*. **36–38**. *P. (P.) ladakhensis*. – Scales: A – head with pronotum and antenna, B – aedeagus.



Figs. 39–59. *Pseudethas* spp., head, pronotum and elytral base, antenna, aedeagus. – **39–41**. *P. (P.) longigenus* n. sp. **42–44**. *P. (P.) afghanicus*. **45–47**. *P. (P.) costatus*. **48–50**. *P. (P.) schawalleri* n. sp. **51–53**. *P. (P.) jaegeri*. **54–56**. *P. (P.) incostatus*. **57–59**. *P. (P.) pakistanus*. – Scales: A – head with pronotum and antenna, B – aedeagus.

wide as pronotum, widest in the middle; ratio elytral length/width 170 : 84; ratio basal width of elytra/basal width of pronotum 52 : 43. Humeral corners rounded (Fig. 39). Keels on 3rd, 5th, 7th and 9th intervals, the other intervals slightly convex. Keels of 3rd, 7th and 9th intervals joined on elytral declivity, keel of 5th interval fading at the tip and not combined with other keels. Elytral intervals very gently punctured and wrinkled, with setae twice as long as the diameter of the punctures. Keels on 5th, 7th and 9th intervals with thick, erect curved setae. Each elytron with 10 rows of punctures; first row with approximately 27 punctures. Epipleura all over its length with one row of punctures slightly decreasing posteriorly; basal punctures as large as on pronotum. – Abdomen: First sternite with rough punctures larger than on epipleural base. Punctures on other sternites gradually decreasing; surface between punctures slightly wrinkled. Setae on ventral side gentle, yellow, twice as long as the diameter of the punctures. – Legs completely yellow-haired. Anterior femora on inner side with very small nodulation, tibiae thin and elongated, male middle and posterior tibiae with a small apical tooth. – Wingless. Aedeagus (Fig. 41): Length approximately 0.84 mm, with two pairs of apical setae.

Diagnosis: *P. longigenus* n. sp. can easily be recognized by its very long genae (longer than eye), the very rough corrugation on head and pronotum, and by the distinct erect and curved hairs on the elytral keels.

Pseudethas (Pseudethas) schawalleri **n. sp.**
(Figs. 13, 48–50)

Holotype (♂): Nepal, Karnali, Jumla to Sisne Himal, 5000 m, 6.–20.VI.1995, leg. J. Kolibáč, SMNS.

Paratypes: Nepal, Dailekh Distr., N Dailekh, 1600 m, 1.–2.VI.1998, leg. W. Schawaller, 3 ♂♂ SMNS.

Etymology: Named after Dr. Wolfgang Schawaller (Stuttgart), collector of part of the type series, who helped me with my first publication.

Description: Body length 3.90–4.05 mm, body width 1.18–1.25 mm. – Body and antennae brown-black, legs and palps rusty-brown or even reddish. – Head (Fig. 48): Ratio length/width 46 : 50, widest before eyes. Eyes divided by cheeks, on inner side with eye keel which is most distinct at middle of eye, dorsal side with about 19 facets in three rows, ventral side with about 10 facets. Tempora widest at posterior margin of eyes, almost straight behind eyes over a distance of about one-quarter eye length, then gradually narrowing towards the cervical constriction. Lateral margins of genae almost parallel. Clypeus slightly convex on anterior margin. Frons with two distinct impressions. Punctulation on vertex rough, finer towards clypeus. Punctures somewhat elongate, with fine, white, anteriorly directed setae as long as punctures. Antennae (Fig. 49) yellow-haired; combined 2nd–11th segments twice as long as width of cervix; ratio of lengths of 2nd–11th segments: 6 : 9.8 : 7.5 : 6.5 : 6 : 6 : 5.5 : 6 : 6.5 : 6.5, ratio of widths: 7 : 7.3 : 7.3 : 7 : 6.7 : 6.7 : 7 : 8.2 : 8.7 : 8; last segment cut latero-apically. – Pronotum (Fig. 48) longer than wide (60 : 55), widest at anterior third, wider than head (55 : 50); ratio widths at posterior edges/at widest point/at anterior edges 43 : 50 : 47. Pronotum in the centre slightly flattened longitudinally, flattening more distinct only in posterior third. Anterior corners gently rounded. Posterior corners obtuse. Punctures on pronotum rough, almost rounded, large and nearly confluent in the middle of the pronotum, smaller laterally; posterior third of lateral margins almost without punctures. Setae of punctures white, anteriorly directed, shorter than diameter of punctures. – Elytra: 2.8 times as long, 1.5 times as wide as pronotum, widest in the middle; ratio elytral length/width 170 : 83. Humeral corners slightly prominent (Fig. 48). Elytral intervals very slightly wrinkled; 3rd, 5th, 7th and 9th intervals keeled (7th and 9th intervals roof-shaped); the other intervals slightly convex or flat. Keel of 5th interval fading on elytral declivity, the other keels fading at their points of fusion. Each elytron with 10 rows of punctures slightly larger than on pronotum; punctures decreasing on elytral declivity, fading posteriorly; first row with about 29 punctures. Epipleura with one row of punctures decreasing posteriorly, very fine near last three sternites. – Abdomen: Punctulation on sternites decreasing towards anal sternite. Punctures on first sternite as large as on elytra, larger than on epipleura; surface between punctures very gently wrinkled. Setae of punctures very fine, as long as diameter of punctures. – Legs: Middle and posterior tibiae of male with distinct apical tooth on inner side. – Wingless. – Aedeagus (Fig. 50): Length approximately 0.75 mm, with a pair of very small apical setae.

Diagnosis: *P. schawalleri* n. sp. is very similar to *P. costatus*, but it shows a different shape of pronotum and genae and has slightly convex non-keeled elytral intervals.

Pseudethas (Pseudethas) thailandicus **n. sp.**
(Figs. 6, 27–29)

Holotype (♂): Thailand, Phetcha Buri Province, 2 km N of Ban Sa Yai Non, 12°56'58"N 99°47'44"E, alt. 40 m, 16.–18.I.2006, leg. S. Bečvář & R. Fouquè, CFR.

Paratypes: Same data as holotype, 2 ♂♂, 1 ♀ CFR, 1 ♂, 1 ♀ HNHM, 1 ♂ SMNS, 1 ♂ CBS.

Etymology: Named after Thailand where the type series was collected.

Description: Body length 2.95–3.40 mm, body width 0.78–0.90 mm. – Body and antennae brown, sometimes rust brown, legs brighter, palps russet. – Head (Fig. 27): Ratio length/width 42 : 43, widest at front margin of eyes. Eyes divided by cheeks, inner side with distinct ocular keel, dorsal side of eye with about 17 facets in three rows, ventral side with about 7 facets. Tempora con-

vex and widest in their anterior third, then narrowing to the cervical constriction. Genae slightly extending from posterior margin of eyes to its widest point at front margin of eyes. Clypeus ogival. Frons with two distinct impressions. Vertex somewhat arched. Punctures of head rounded, with short light-yellow anteriorly directed setae, rough on vertex, fading towards clypeus; surface between punctures smaller than diameter of the punctures. Antennae (Fig. 28) distally with short light-yellow hairs; combined 2nd–11th segments twice as long as posterior width of pronotum; ratio of lengths of 2nd–11th segments: 6 : 8.1 : 6.5 : 6 : 6 : 6 : 6.5 : 6.8 : 7.3 : 6.8, ratio of widths: 6.5 : 6 : 6 : 6 : 6.5 : 6.5 : 6.8 : 7 : 7.6 : 7; last segment cut latero-apically. – Pronotum (Fig. 27) as wide as head, much longer than wide (50 : 43), widest at anterior quarter; ratio widths at posterior edges/at widest point/at anterior edges 35 : 43 : 37. Anterior corners slightly prominent, rounded. Posterior corners rectangular. Lateral margin of pronotum concave before posterior edges. Pronotum with a longitudinal medial impression which is less distinct near anterior and posterior margins of pronotum. Pronotal base slightly convex. Punctures on pronotum larger than on head, almost rounded, dense but not confluent, somewhat smaller and denser on anterior margin; setae as long as on head but less regular. Lateral margin of pronotum approximately as wide as diameter of punctures, without punctulation. – Elytra: 2.6 times as long, 1.4 times as wide as pronotum; ratio elytral length/width 129 : 60; ratio basal width of elytra/basal width of pronotum 40 : 35. Humeral corners slightly prominent (Fig. 27). Lateral margins straight from first quarter to their maximal width at the end of second third. 3rd, 5th, 7th and 9th elytral intervals keeled, 7th and 9th roof-shaped, 3rd less convex on disk, the other intervals very slightly convex or flattened. Keels of 3rd and 7th intervals joined on elytral declivity, keel of 9th interval fading at the tip and not combined with other keels. Each elytron with 10 rows of punctures, near base as large as on pronotum, gradually decreasing posteriorly; punctures rounded at elytral base, slightly elongated on disk and elytral declivity; first row with approximately 36 punctures. Elytral intervals very gently wrinkled. Elytral keels with a row of bright, very fine recumbent setae. Epipleura with one row of somewhat elongated punctures which are smaller on epipleural base than on elytral base, gradually decreasing posteriorly, fading towards anal sternite. – Abdomen: First sternite rarely with punctures of same size as on elytral base. Punctulation of sternites gradually decreasing from first sternite to anal sternite, denser posteriorly. Light-yellow setae on ventral side of abdomen gentle, increasing in length from anal sternite towards metasternum. – Legs: Femora without teeths, claviform distally; male middle and posterior tibiae with small tooth. – Wingless. – Aedeagus (Fig. 29): Length approximately 0.46 mm; a very gentle seta on each side apically.

Diagnosis: *P. thailandicus* n. sp. has a complete longitudinal pronotal impression like *P. antennalis*, *P. ladakhensis*, *P. nepalicus*, *P. quadraticeps*, and *P. rogersi*. It is, however, narrower and smaller than those five species.

Remarks: This species was collected under stones, under a piece of wood and under a fallen abandoned ant-nest of the genus *Crematogaster*. Additional Tenebrionidae of the same tribe Stenonsini, namely *Stenosis herberti* Kulzer, 1960, *Gebieniella stenosides* (Pascoe, 1862) and *Dichillus kuschstaberi* Kaszab, 1981 have been collected at the same locality (see Fig. 60).

Pseudethas (Stenillus) weigeli **n. sp.**
(Figs. 3, 19–21)

Holotype (♂): Nepal, Prov. Bheri, Distr. Surkhet, 20 km N Surkhet, 2000 m, 1.VI.1995, leg. A. Weigel, SMNS.

Paratype: W Nepal, Distr. Jumla, Rimi to Chaurikot, 2800–3000 m, 5.VI.1997, leg. A. Weigel, 1 ♀ NKME.

Etymology: Named after Andreas Weigel (Wernburg, Germany), specialist for Cerambycidae and collector of the type series.

Description: Body length 3.8–4.3 mm, body width 1.15–1.35 mm. – Body dark-brown; legs, antennae and palps slightly brighter. – Head (Fig. 19): Ratio length/width 43 : 48, widest at front margin of eyes. Eyes completely divided by cheeks, dorsal side of eye with about 17 facets in three rows, ventral side with about 11 facets. Tempora very slightly narrowing over a distance of about half eye length, then gradually narrowing towards cervical constriction. Genae almost parallel over a distance of slightly less than two eye lengths. Clypeus almost straight. Two impressions on frons. Punctulation on vertex rough, somewhat elongated, punctures on clypeus smaller and rounded; surface between punctures slightly wrinkled. Setae fine, approximately of same length as diameter of punctures. Antennae (Fig. 20) lightly haired, setae as long as half length of middle segments; combined 2nd–11th segments 1.5 times as long as width of head; ratio of lengths of 2nd–11th segments: 6 : 8.4 : 6 : 5.6 : 4.6 : 5 : 5.3 : 5.5 : 6.6 : 7.6, ratio of widths: 5 : 5.3 : 5.3 : 5.5 : 5.5 : 6 : 6.3 : 7 : 7.5 : 7. – Pronotum (Fig. 19) considerably wider than head (60 : 48), widest at anterior quarter; ratio length/width 60 : 60; ratio widths at posterior edges/at widest point/at anterior edges 45 : 60 : 51. Anterior corners slightly overlapping, rounded. Posterior corners obtuse. Lateral margin of pronotum slightly concave near posterior corners. Pronotal disk slightly flattened. Punctures on disk elongated, larger than on head; rounded and denser around disk; surface between punctures slightly wrinkled. Pronotum haired with fine yellow setae which are slightly longer than diameter of punctures. – Elytra: 2.7 times as long, 1.4 times as wide as pronotum, widest in the middle; ratio elytral length/width 160 : 83; ratio basal width of elytra/basal width of prono-

Fig. 60. Type locality of *Pseudethas thailandicus* n. sp. (Thailand, Phetcha Buri Province, 2 km N of Ban Sa Yai Non, 12°56'58"N 99°47'44"E, alt. 40 m, I.2006), where also *Stenosis herberti*, *Gebieniella stenosides* and *Dichillus kuschstaberi* have been collected.

tum 49 : 45. Base of elytra distinctly concave. Humeral corners rounded (Fig. 19). All elytral intervals slightly convex, 7th and 9th intervals somewhat more convex, 8th interval less convex. Each elytral interval with one row of very fine punctures with fine bright setae twice as long as diameter of larger punctures. Each elytron with 10 rows of oval punctures, as long as on vertex of head; first row with about 27 punctures. Epipleura with one row of elongated punctures as large as on dorsal part of elytra, punctures fading towards anal sternite. – Abdomen: Punctures of sternites decreasing from first sternite, where there are rough, rounded and somewhat larger than on epipleura, towards anal sternite, where there are smallest and densest. Sternites lightly haired, setae slightly longer than diameter of punctures. – Legs: Male middle and posterior tibiae on inner side with distinct tooth. – Wingless. – Aedeagus (Fig. 21): Length approximately 0.8 mm, with a pair of fine apical setae.

Diagnosis: *P. weigeli* n. sp. belongs to the subgenus *Stenillus* because of the shape of the tempora and the moderately convex elytral intervals. It differs from the only other species of this subgenus, *P. (S.) monticola*, mainly by the shape of the pronotum.

5 Key to the species of *Pseudethas*

1 Tempora widest at posterior margin of eye, gradually narrowing towards cervix. Pronotum at most with a slight flattening in its posterior third. 1st–6th elytral intervals only slightly convex, 7th–9th intervals convex. . . . . subgenus *Stenillus* **2**

– Tempora usually convex or at least parallel, constricted towards cervix, often overlapping lateral margins of eyes. Pronotum medially with a longitudinal impression, sometimes only very slightly developed in its posterior third. 3rd, 5th, 7th and 9th elytral intervals (sometimes only lateral intervals) often strongly convex. . . . . subgenus *Pseudethas* **3**

2 Pronotum almost quadrate, slightly convex, flattened on lateral margins. Pronotal punctulation gentle, elongated. Elytral intervals with several irregular rows of very gentle punctures. Aedeagus unknown. Body length 4.1 mm. (Figs. 2, 17–18). . . . . ***monticola***

– Pronotum heart-shaped, strongly convex, only slightly flattened on lateral margins. Punctulation on pronotum larger and rounder. Elytral intervals with only one row of very fine punctures. Aedeagus see Fig. 21. Body length 3.8–4.3 mm. (Figs. 3, 19–21). . . . . ***weigeli* n. sp.**

3 Pronotum with a complete longitudinal medial impression. **4**

– Pronotal impression very faint or restricted to the posterior third of the pronotum. **9**

4 3rd elytral interval convex over is whole length. First elytral row with about 33 punctures. **5**

– 3rd elytral interval convex only at base, then flattened. First elytral row with about 36–43 punctures. **6**

5 Keel of 7th elytral interval almost straight in dorsal view. Elytra widest behind middle. 4th and 6th elytral intervals flat. 2nd elytral interval very gently wrinkled, with a row of very fine punctures without setae. Elytral punctures fine, distance between punctures of a row almost as long as a puncture. Aedeagus unknown. Body length 3.7–4.0 mm. (Figs. 4, 22–23). . . . . ***quadraticeps***

– Keel of 7th elytral interval curved in dorsal view. Elytra widest at middle. 4th and 6th elytral intervals gently convex. 2nd interval not wrinkled, with a row of very fine punctures with long fine setae. Elytral punctures very rough, deeply impressed, distance between punctures of a row about half as long as a puncture. Aedeagus see Fig. 26. Body length 3.4–3.9 mm. (Figs. 5, 24–26). . . . . ***nepalicus***

6 Body small and narrow. Body length 2.95–3.40 mm, body width 0.78–0.90 mm. Ratio pronotum length/width approximately 1.15 : 1. – First elytral row with about 36 punctures. Aedeagus see Fig. 29. (Figs. 6, 27–29). . . ***thailandicus* n. sp.**

– Body length 3.3–4.8 mm, body width 1.05–1.40 mm. Ratio pronotum length/width close to 1 : 1. . . . . **7**

7 Elytral margins parallel over most of their length. 3rd–8th and 11th antennal segments almost of same width. – First elytral row with about 43 punctures. Aedeagus see Fig. 32. Body length 3.8–4.8 mm. (Figs. 7, 30–32). . . . . ***antennalis***

– Elytral margins rounded or parallel only over a short distance. 3rd–8th antennal segments slightly extending towards apex, 11th antennal segment wider than 8th one. **8**

8 Tempora suddenly constricted towards cervix. Genae extended, widest before eyes. Humeral corners overlapping elytral base. Pronotal base at level of 6th elytral interval. First elytral row with about 43 punctures. Aedeagus see Fig. 35. Body length 3.3–3.9 mm. (Figs. 8, 33–35). . . . . ***rogersi***

– Tempora gradually narrowing towards cervix. Genae not extended, widest at level of eyes. Humeral corners not overlapping elytral base. Pronotal base at level of 6th row of punctures. First elytral row with about 36 punctures. Aedeagus see Fig. 38. Body length 3.6–4.1 mm. (Figs. 9, 36–38). . . . . ***ladakhensis***

9 3rd, 5th, 7th and 9th elytral intervals keel-like, different from the other intervals; the 3rd interval can be flattened and is more or less keel-like only at base. **10**

– All elytral intervals convex or flat in the same way. Only lateral intervals slightly convex. **13**

10 Tempora almost parallel. Distance between elytral punctures as wide as a puncture. Body haired. **11**

– Tempora convex. Distance between elytral punctures somewhat wider than a puncture. Body not haired or at most with very short and scattered hairs. **12**

11 Keels of 5th, 7th and 9th elytral intervals with erect curved setae. Head and pronotum very roughly wrinkled between punctures. Pronotum widest at first quarter. Elytral humeral corners prominent. Tibiae elongate, posterior tibia as long as maximum width of pronotum. Aedeagus see Fig. 41. Body length 4.0 mm. (Figs. 10, 39–41). . . . . ***longigenus* n. sp.**

– Keels of 5th, 7th and 9th intervals with recumbent hairs. Head and pronotum gently wrinkled between punctures. Pronotum widest at first third. Elytral humeral corners rounded. Tibiae short, posterior tibia as long as width of pronotum at posterior corners. Aedeagus see Fig. 44. Body length 3.4–3.7 mm. (Figs. 11, 42–44). . . . . ***afghanicus***

12 Genae rounded near middle of eyes. Pronotum long, heart-shaped, pronotal base distinctly narrower than elytral base. Elytral humeral corners strongly prominent. Non-keeled elytral intervals flat. Aedeagus see Fig. 47. Body length 4.0–4.8 mm. (Figs. 12, 45–47). . . . . ***costatus***

– Genae parallel at sides of eyes. Pronotum almost quadrate, pronotal base only slightly narrower than distance of elytra between humeral corners. Elytral humeral corners less prominent. Non-keeled elytral intervals slightly convex. Aedeagus see Fig. 50. Body length 3.90–4.05 mm. (Figs. 13, 48–50). . . . . ***schawalleri* n. sp.**

13 Body deep black, glabrous. Elytra with rows of very fine punctures. Elytral intervals flat, only lateral ones slighty convex. Aedeagus see Fig. 53. Body length 3.8–4.1 mm. (Figs. 14, 51–53). . . . . ***jaegeri***

– Body brown to russet, haired. Elytra with rows of rougher punctures. Medial elytral intervals slightly convex, lateral ones more convex. **14**

14 Genae rounded. Tempora convex, as long as the eye. Head and pronotum wrinkled between punctures. Pronotum strongly convex. Aedeagus see Fig. 56. Body length 3.0–4.0 mm. (Figs. 15, 54–56). . . . . ***incostatus***

– Genae parallel. Tempora convex, shorter than the eye. Head and pronotum almost glabrous between punctures. Pronotum less convex. Aedeagus see Fig. 59. Body length 2.7–3.4 mm. (Figs. 16, 57–59). . . . . ***pakistanus***

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Manuscript received: 30.I.2007, accepted: 19.IV.2007.

A new species of *Tribolium* Macleay from Namibia (Coleoptera: Tenebrionidae: Triboliini)

Roland Grimm

Abstract

Tribolium namibiensis **n. sp.** from Namibia is described and compared with *T. sulmo* Hinton, 1948. A checklist of the species of the genus *Tribolium* Macleay, 1825 is presented.

Keywords: Tenebrionidae, *Tribolium*, new species, taxonomy, checklist, Namibia.

Zusammenfassung

Tribolium namibiensis **n. sp.** aus Namibia wird beschrieben und mit *T. sulmo* Hinton, 1948 verglichen. Eine Checkliste der Arten der Gattung *Tribolium* Macleay, 1825 wird erstellt.

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1 Introduction

The genus *Tribolium* Macleay, 1825 is a member of the tribe Triboliini, subfamily Tenebrioninae (Bouchard et al. 2005). According to Hinton (1948), the type species is *Colydium castaneum* Herbst, 1797.

Hinton (1948) published a synopsis of the genus and listed 26 species. According to this paper *Tribolium risbeci* described by Lepesme (1943) is a damaged specimen of *Alphitobius laevigatus* (Fabricius, 1781). Subsequently additional species were described by Gridelli (1950), Neboiss (1962), Nakane (1963), Halstead (1969), Triplehorn (1978), Kaszab (1982), and Grimm (2001). Taxonomical changes were indicated by Halstead (1967a, b) and Grimm (2001).

A new species of *Tribolium* from Namibia is described in the present paper, and a checklist of all species of the genus *Tribolium* is provided (Tab. 1), including distributional data.

Acknowledgements

Cordial thanks are due to Dr. Wolfgang Schawaller (Stuttgart) for the loan of material under his care and for reading the manuscript. Thanks are extended to Dr. Ottó Merkl (Budapest) for reviewing the manuscript and Johannes Reibnitz (Stuttgart) for producing the photographs.

2 *Tribolium namibiensis* n. sp.

Holotype: ♂, N Namibia, 45 km SE Okakarara, Farm Dieckmann, at light, 1300 m, 24.–25.IV.2005, leg. W. Schawaller; Staatliches Museum für Naturkunde, Stuttgart.

Paratypes: Same data as holotype; 1 specimen in Staatliches Museum für Naturkunde, Stuttgart; 1 specimen in Transvaal Museum, Pretoria.

Etymology

Named after Namibia where the type series was collected.

Description

Body (Fig. 1) subparallel, moderately convex, with elytral disc nearly flat; dark reddish brown, only feebly shining. Body length 3.75–4.25 mm, body width 1.35–1.65 mm.

Head widest at about middle of genae; punctures distinct, round or nearly so, usually separated by less than one half puncture diameter; surface between punctures with micro-reticulation, appearing almost matt; margin above eye flexed upwards, ridge-like. Clypeus with anterior margin very feebly emarginated, nearly truncate; surface sculptured like middle of head, but with punctures slightly smaller. Narrowest part of eye where divided by genal canthus as broad as three facets; eyes separated ventrally by more than the transverse diameter of ventral part of eye. Antenna with club abruptly 5-segmented.

Pronotum broadest at about middle, transverse convex, width/length ratio 1.42–1.48 (measured in each case in the middle), base broader than apex. Sides arched and distinctly sinuate before posterior angles which are prominent; anterior angles projecting beyond apex. Lateral sides margined, apex unmargined, but with sides curved inwards at apex so that the extreme lateral part of apex appears to be margined. Disk with mostly round punctures,

Tab. 1. Checklist and distribution of the species of *Tribolium* Macleay.

Species	Distribution
T. alcine Hinton, 1948	Madagascar
T. anaphe Hinton, 1948	Africa south of Sahara
T. antennatum Hinton, 1948	Australia: Queensland
T. apiculum Neboiss, 1962	Australia: Queensland
T. arndti Grimm, 2001	South Africa
T. audax Halstead, 1968	North America
T. beccarii Gridelli, 1950	Niger
T. bremeri Grimm, 2001	South Africa
T. brevicornis (LeConte, 1859)	USA: Western United States
T. carinatum Hinton, 1948 *T. c.* ssp. *dubium* Hinton, 1948	Argentina
T. castaneum (Herbst, 1797)	Cosmopolitan
T. ceto Hinton, 1948	Madagascar
T. confusum Jacquelin Du Val, 1868	Cosmopolitan
T. cylindricum Hinton, 1948	Southeast Asia
T. destructor Uyttenboogaart, 1934	Africa, Europe, North America
T. downesi Hinton, 1948	Chad, Mali, Sudan
T. ferreri Grimm, 2001	The Gambia
T. freemani Hinton, 1948	Kashmir
T. gebieni Uyttenboogaart, 1934	Brazil, Paraguay
T. indicum Blair, 1930 syn. *T. indicum* f. *ares* Hinton, 1948 syn. *T. indicum* f. *seres* Hinton, 1948	Western, central and eastern Africa, Saudi Arabia, Iran, India
T. linsleyi Hinton, 1948	Mexico
T. madens (Charpentiers, 1825)	Cosmopolitan
T. myrmecophilum Lea, 1904	Australia: Victoria
T. namibiensis n. sp.	Namibia
T. parallelum (Casey, 1890)	USA: Western United States
T. parki Hinton, 1948	Indonesia: Larat (Tanimbar Islands), Bali; Maluku
T. politum Hinton, 1948	Indonesia: Durian (Riau Islands)
T. quadricollis (Fairmaire, 1902) syn. *T. dolon* Hinton, 1948	Madagascar
T. semele Hinton, 1948	Mauretania, Mali, Chad, Sudan
T. semicostatum (Gebien, 1910) syn. *T. giganteum* Hinton, 1948	Kenya
T. setosum Triplehorn, 1978	USA: Arizona
T. sulmo Hinton, 1948	The Gambia, Ghana, Ethiopia
T. thusa Hinton, 1948	Chad, Namibia, South Africa, Botswana
T. uezumii Nakane, 1963	Japan
T. waterhousei Hinton, 1948	Australia: New South Wales, Queensland

separated by a distance of a half to one puncture diameter, with many punctures on mid-disc region separated by one diameter; punctures at sides always separated by less than one diameter; surface between punctures weakly micro-reticulated.

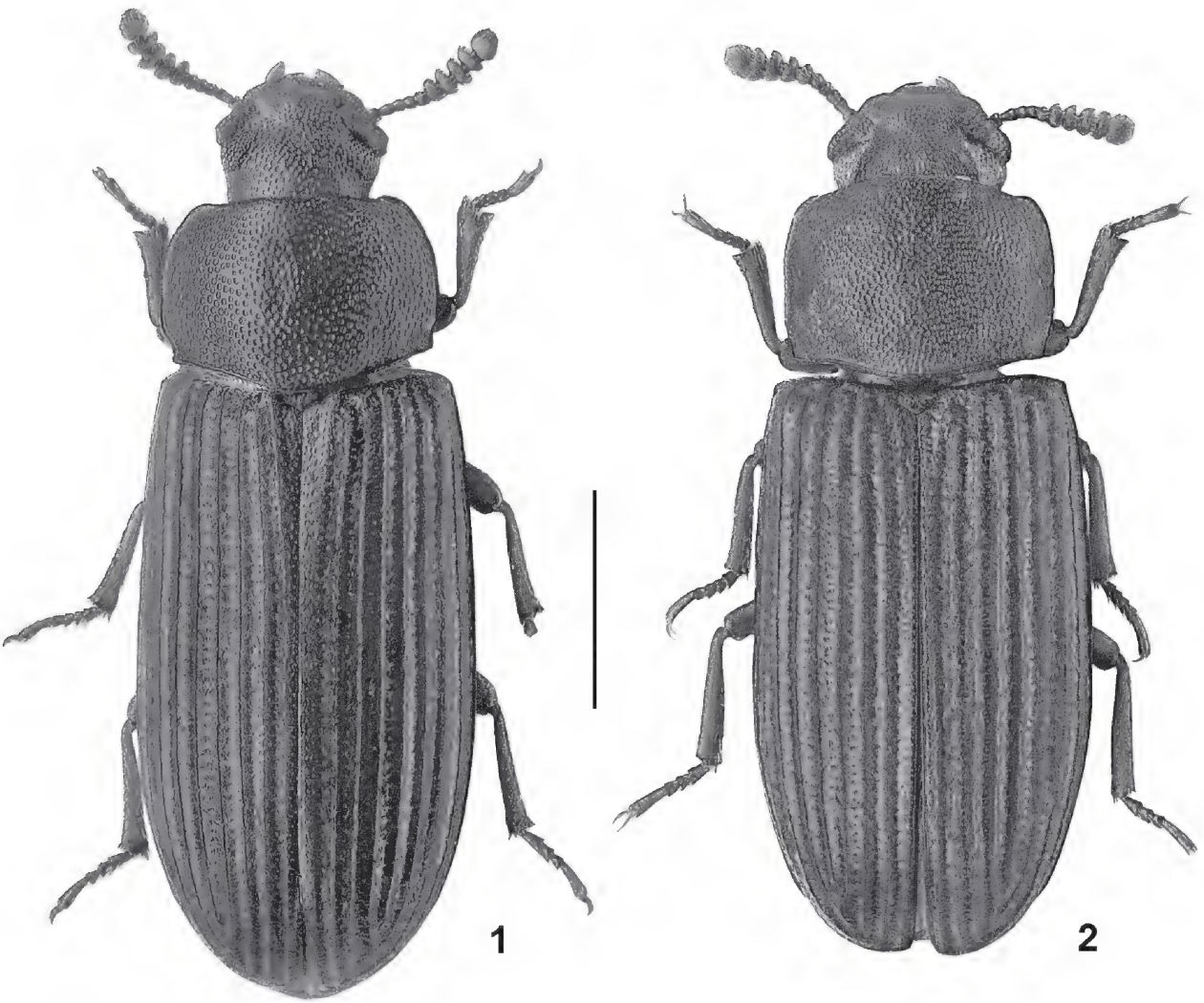
Elytra with intervals 2–9 strongly carinate from base to apex, sutural interval flat on disk but distinctly carinate near base and apex. Discal strial punctures arranged in rather irregular rows and longitudinally separated mostly by one to two diameters; intervals with indistinct punctures smaller than strial punctures near the top of carinae, and with numerous shallow, transverse or oblique wrinkles.

Prosternum with coarse but mostly round punctures, mostly separated by less than one diameter. Metasternum with punctures on disc separated by 2–4 puncture diameters, coarser and denser on sides; punctures of abdominal sternites similar, separated by 1–2 diameters on disc and somewhat denser on sides. Fifth sternite with a very fine and indistinct apical marginal line.

Aedeagus see Fig. 3.

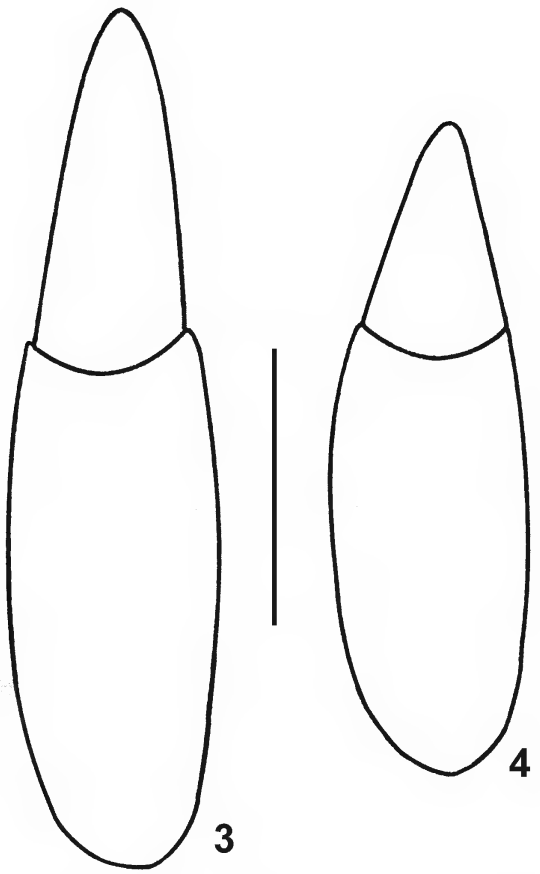
Comparison

T. namibiensis n. sp. (Fig. 1) is quite similar in general appearance to *T. sulmo* Hinton, 1948 (Fig. 2), but may be easily distinguished as follows: Pronotum slightly more



Figs. 1–2. *Tribolium* spp., dorsal view. – **1**. *T. namibiensis* n. sp., holotype. **2**. *T. sulmo* Hinton, non-type from The Gambia. – Scale: 1 mm.

convex with puncturation shallower, but slightly larger and less dense; space between punctures wider and even (in *T. sulmo* the punctures are smaller, denser and deeper; the space between punctures appearing ridge-like). The fused parameres of the aedeagus are longer in *T. namibiensis* n. sp. (Fig. 3), shorter and stouter in *T. sulmo* (Fig. 4).



Figs. 3–4. *Tribolium* spp., aedeagus, dorsal view. – **3**. *T. namibiensis* n. sp. **4**. *T. sulmo* Hinton. – Scale: 0.2 mm.

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Manuscript received: 13.VIII.2007, accepted: 20.IX.2007.

Guanobius borneensis n. gen., n. sp. from Borneo (Coleoptera: Tenebrionidae: Alphitobiini)

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Abstract

The tenebrionid beetle *Guanobius borneensis* **n. gen.**, **n. sp.** is described from caves in Borneo. *Guanobius* **n. gen.** is similar to *Alphitobius* Stephens, but differs in size, shape of head, form of clypeus, genae on underside of head as well as the obliterated primary structure of elytra. The asymmetrical base of the aedeagus, which is protruded ventrad on the left, is discussed and considered as a possible autapomorphic character of the tribe Alphitobiini.

Keywords: Tenebrionidae, Alphitobiini, Borneo, Malaysia, Sabah, Sarawak, new genus, new species, phylogeny, cave beetle.

Zusammenfassung

Der Schwarzkäfer *Guanobius borneensis* **n. gen.**, **n. sp.** aus Höhlen in Borneo wird beschrieben. *Guanobius* **n. gen.** unterscheidet sich von der ähnlichen Gatttung *Alphitobius* Stephens durch die Größe, die Form und Gestalt von Kopf und Clypeus, die Wangen auf der Unterseite des Kopfes sowie die verwischte primäre Struktur der Oberseite der Flügeldecken. Es ist möglich, dass die an der linken Seite nach unten vorgezogene, asymmetrische Basis des Aedoeagus ein autapomorphes Merkmal der Tribus Alphitobiini darstellt.

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1 Introduction

A few years ago, the author received some specimens of an unknown darkling beetle collected by Dr. K. Handke (Ganderkesee) in the Gomantong Caves in Sabah (Malaysia, Borneo). In 2007 the author had the chance to visit the caves and to collect a larger series of this strange species. It is common in the faeces of bats and cave swifts in which the larvae dwell. One specimen was caught in Tambunan (Sabah) at light. Additional specimens originating from other caves were discovered by Dr. W. Schawaller (Stuttgart) in the collections of the BMNH.

According to Doyen (1989), Doyen et al. (1989), and Aalbu et al. (2002) the tribe Alphitobiini Reitter, 1917 (subfamily Tenebrioninae) includes the genera *Alphitobius* Stephens, 1829, *Diaclina* Jacquelin Du Val, 1861, and *Metaclisa* Jacquelin Du Val, 1861. Bremer (1992) pointed out that some genera of the Ulomini sensu Gebien (1940), i. e. *Alphitobius*, *Diaclina*, *Epipedodema* Gebien, 1920, and *Donisellus* Bremer, 1992, are characterized by the asymmetrical base of the aedeagus which is protruded ventrad on the left. This fact is also true for the new genus.

Acronyms of depositories

BMNH	Natural History Museum, London, United Kingdom
CKH	Collection Dr. Klaus Handke, Ganderkesee, Germany
CRG	Collection Dr. Roland Grimm, Tübingen, Germany
HNHM	Hungarian Natural History Museum, Budapest, Hungary
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZSM	Zoologische Staatssammlung, München, Germany

Acknowledgements

For the gift and/or loan of material I thank Drs. M. Baehr (ZSM), M. Barclay (BMNH), K. Handke (Ganderkesee), and W. Schawaller (SMNS). J. Reibnitz (SMNS) kindly produced the photograph. Furthermore, I am grateful to Drs. O. Merkl (HNHM) and W. Schawaller for reviewing the manuscript.

2 Description of *Guanobius borneensis* n. gen., n. sp.

2.1 *Guanobius* n. gen.

(Figs. 1, 3)

Type species: *Guanobius borneensis* n. sp.

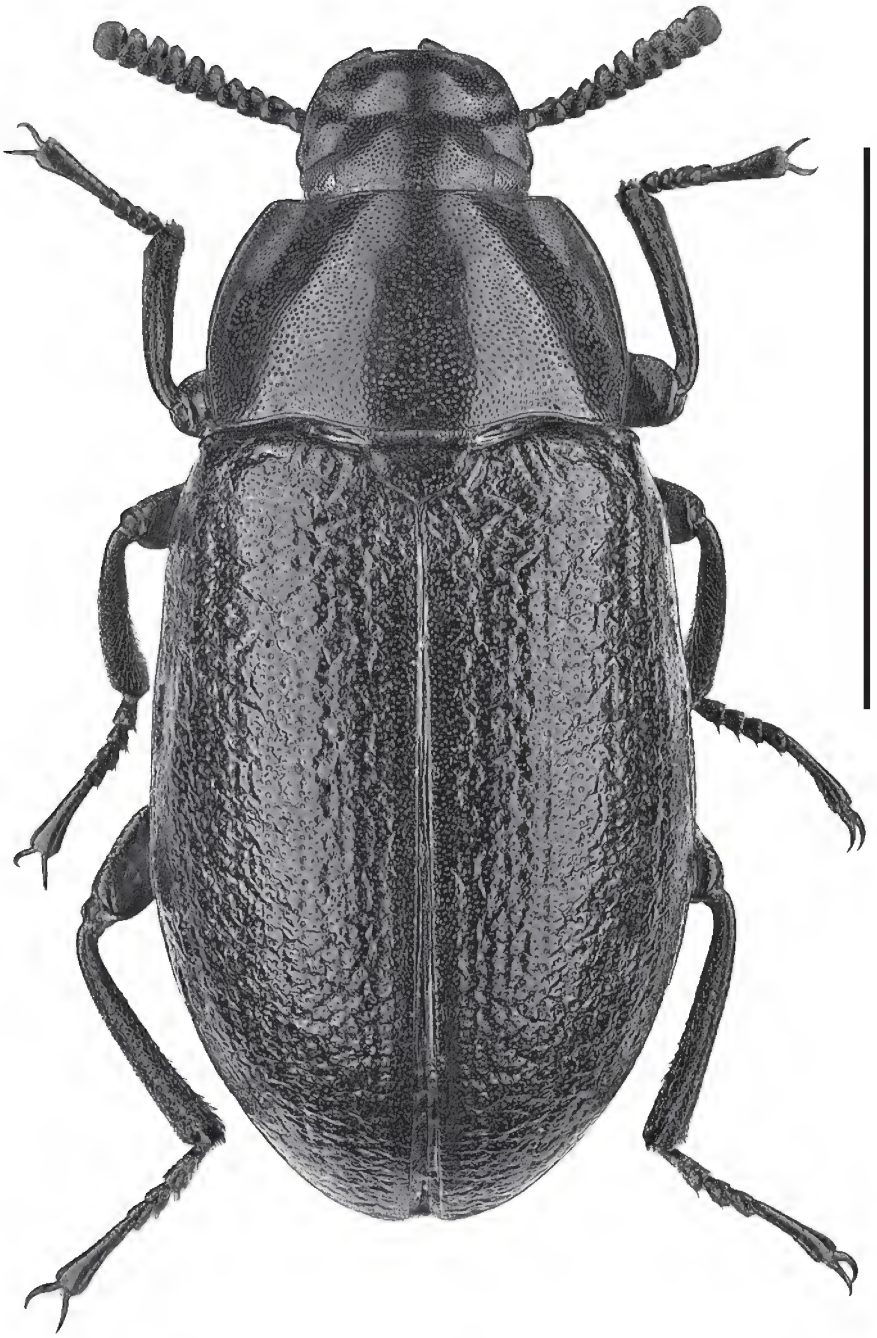


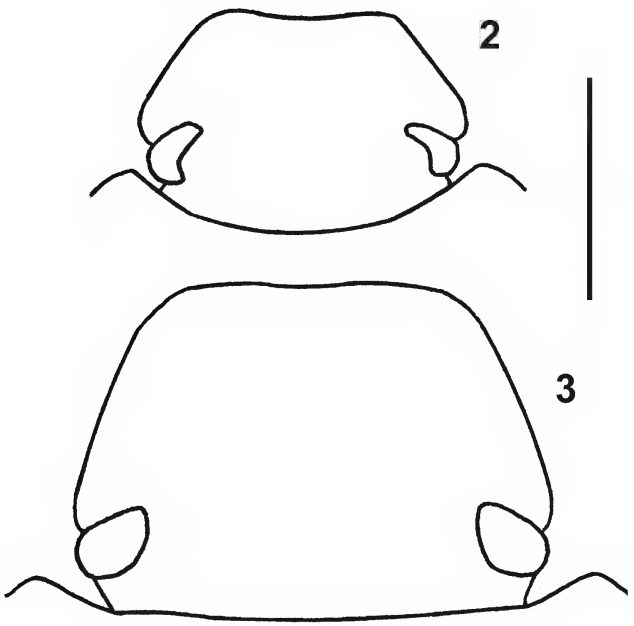
Fig. 1. *Guanobius borneensis* n. gen., n. sp., dorsal view, holotype. – Scale: 5 mm.

Etymology

Combination of guano (accumulated excrements of birds and bats) and Greek *bios* (place of residence).

Diagnosis

Body length 10–12 mm; hind wings developed. Head (Fig. 3) subtrapezoidal, with clypeus slightly bent up; labrum about 2.5 times as wide as long, with the labroclypeal membrane concealed; mandible with bifid incisors; eyes emarginate by genal canthus; genae in front of eyes about as broad as eyes; antenna incrassate, bearing compound sensoria on apical six segments; genae on underside of head besides eye with a tooth-like protrusion; mentum without protuberance. Pronotum wider than long,



Figs. 2–3. Shape of head. – **2**. *Alphitobius diaperinus* (Panzer, 1797). **3**. *Guanobius borneensis* n. gen., n. sp. – Scale: 0.5 mm.

widest in front of base, convex, with lateral borders separated from the discal convexity by a narrow submarginal depression running in line with the lateral border; prosternal process bent down behind coxa, distant from mesosternal cavity. Elytra with nine striae, scutellary striole present; covered with wrinkles eliminating the primary structure of the striae and interstriae; humeral angle prominent; lateral margination visible from above throughout whole length; pseudopleuron complete, apical part with crested outer border. Process of first abdominal segment acute; femora surpassing the lateral border of the elytra. Protibia with its outer edge bluntly rounded, only slightly dilated towards apex. Abdominal sternites 3 and 4 with exposed intersegmental membrane. Aedeagus not inverted, with an asymmetrical base.

Remarks

The new genus (Figs. 1, 3) is similar to *Alphitobius* (Fig. 2) but differs by larger size (*Alphitobius* 5–8 mm), the shape of the head (compare Figs. 2 and 3) and slightly bent up border of the clypeus, protruding genae on the underside of the head, obliterated striae and wrinkled surface of the elytra, and bluntly rounded outer side of the protibia (in *Alphitobius* edging at least indicated). As far as known, *Alphitobius* is an Ethiopian faunal element, though two synanthropic species are known to be cosmopolitans.

2.2 *Guanobius borneensis* **n. sp.**
(Figs. 1, 3–7)

Holotype: ♂, Borneo (Malaysia, Sabah), S Sandakan, Gomantong Caves, 13.III.2007, R. Grimm leg. (CRG).

Paratypes: Same data as holotype, 68 specimens (CRG), 7 specimens (SMNS), 5 specimens (ZSM), 2 specimens (HNHM). – Borneo (Malaysia, Sabah), Tambunan, 500 m, at light, 28.–31.III.2007, R. Grimm leg., 1 specimen (CRG). – Borneo (Malaysia, Sabah), Gomantong Caves, 3.–22.IV.1995, K. Handke leg., 5 specimens (CKH). – Borneo (Malaysia, Sarawak), Gunung Mulu National Park, R. G. S. Exped. 1977-8, J. D. Holloway et al., B. M. 1978-206, Deer Cave, 19.VI.1978, V. F. Eastop, 2 specimens (BMNH). – Borneo (Malaysia, Sabah), SSE. Telupid, R. Karamuak, 0 m, 200 ft., 1.–7.IX.1977, Dampbat & Swift dung, M. E. Bacchus, B. M. 1978-48, 3 specimens (BMNH).

Etymology

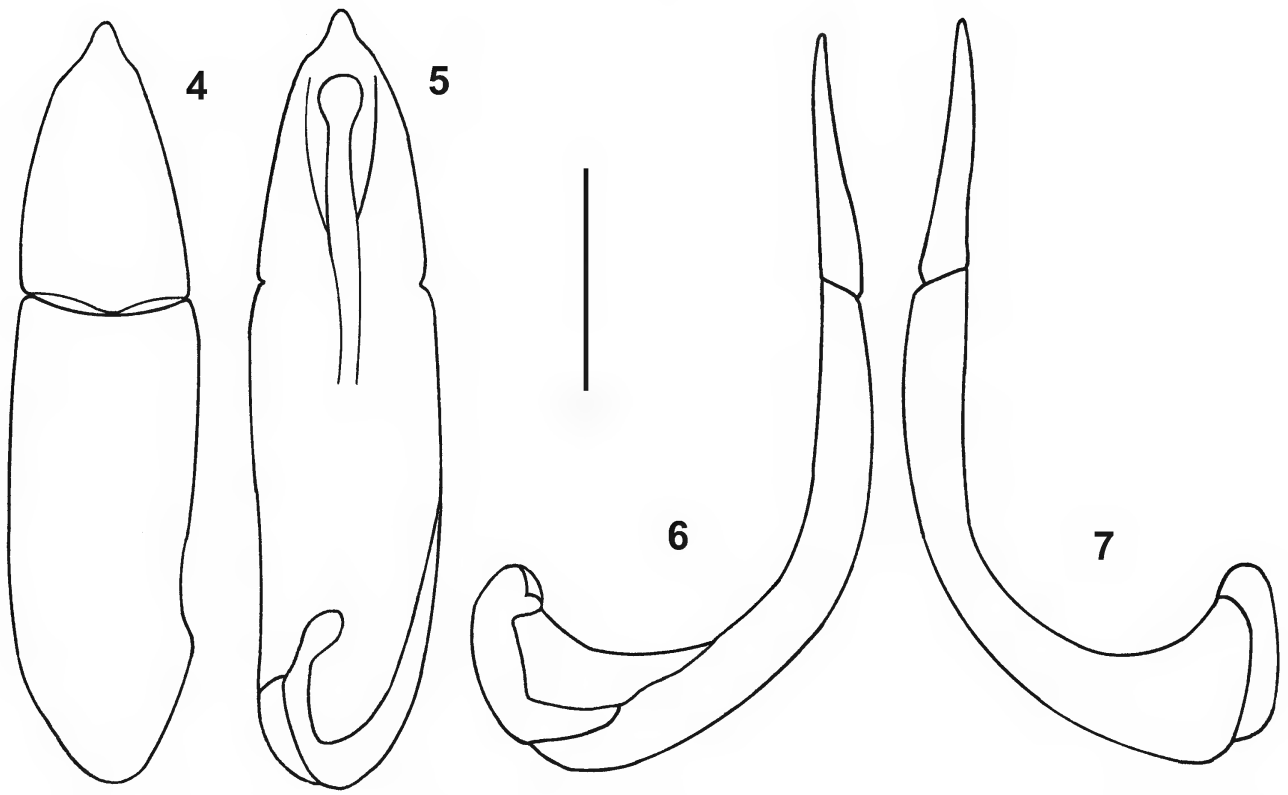
Named after the island of Borneo where the type series was collected.

Description

Black to blackish brown, shining, appendages in part and underside occasionally castaneous. Body length 10.0–11.8 mm, width at broadest point behind middle of elytra 4.5–5.3 mm.

Head (Fig. 3) sub-trapezoidal, puncturation coarser and denser on vertex and frons, but finer and sparser on clypeus. Fronto-clypeal suture distinct; clypeus slightly convex, its border weakly bent up, feebly emarginated in the middle and there thinner than lateral parts when seen from the front; outline continuous, not interrupted between clypeus and front. Eyes large, constricted by genal canthus, dorsal part smaller than ventral part. Genae in front of eyes with an impression, about as wide as eyes, genal canthus not projecting outwards beyond contour of eye; underside of head beside eye with a tooth-like protrusion. Submentum broader than long, trapezoidal, narrowed towards base, pubescent; anterior border shallowly emarginated. Apical palpomere of maxillary palpi axe-shaped. Antennae thickened, proximal four antennomeres simple, the following ones serrate.

Pronotum transverse convex, width/length ratio 1.64–1.79 (width measured at widest point, length in the middle), widest between middle and base, with dense and fine, mostly round punctures as on vertex; sides shallowly rounded, narrower towards anterior than to posterior border; anterior border shallowly emarginated, posterior border bisinuate; all borders margined, lateral borders and lateral parts of posterior border carinate and separated from discal convexity by a narrow submarginal depression running in line with border; anterior border with fine carinula at sides; anterior angles rectangular, posterior angles obtuse. A shallow, roundish impression in the middle of the sloping lateral surface, close to lateral border, and a very fine, median linear longitudinal impression or line present; besides this line sometimes with an addi-



Figs. 4–7. *Guanobius borneensis* n. gen., n. sp., aedeagus. – **4**. Dorsal view. **5**. Ventral view. **6**. Lateral view, left side. **7**. Lateral view, right side. – Scale: 0.5 mm.

tional shallow roundish impression in the middle. Propleuron with interrupted longitudinal wrinkles and with fine scattered pubescence; border mainly even, with interspersed punctures; prosternum rough; prosternal process pubescent, with apical portion bent downwards between procoxal cavities, flat and broadened at apex.

Elytra convex, wider than pronotum, with faintly rounded, almost sub-parallel sides; humeral angles obtuse, distinct; sides gradually and faintly dilated backwards, including the point of greatest width behind middle, then rounded and strongly narrowed towards apex, the latter rounded. Scutellum large, triangular, punctured. Elytra with nine striae, scutellary striole present; punctures of rows like those of pronotum, the interstriae between the rows slightly convex, much broader than the rows and covered with punctures a little finer than those of the rows, bearing very fine, small setae; along the sides with a very fine and narrow sub-marginal depression, the lateral margination visible from above; whole surface covered with wrinkles eliminating the primary structure of the striae and interspaces. Pseudopleura slightly narrowed from base to about middle, then almost parallel towards the apex, and in front of the apex again narrowed; carinate laterally in about distal half, and covered with dense, fine rough punctures. Mesosternum depressed apically, with a smooth, oblong triangular, backwards broadened median part, and with a dense and rough, rugose punctation on the sides. Metasternum longer than first abdominal sternite, with dense coarse punctures and dense pubescence; posterior border in front of metacoxal cavity broadly margined by a deep transverse groove; anterior border in the middle strongly margined; a small depression in front of process of first abdominal segment covered with very fine dense microgranulation beside the visible part of metasternal suture. Abdominal sternites dense, coarsely punctured, pubescent. Fifth abdominal sternite in the middle near its base with a very shallow rounded impression.

Legs without modifications; femora compressed, with underside laterally carinate, and slightly excavate, dilated towards apex; tibiae rounded, without any spines or crenulation; tarsi slender.

Aedeagus (Figs. 4–7) with an asymmetrical base.

No external sexual dimorphism.

Habitat

Dwelling in caves, in the faeces of bats and cave swifts.

Distribution

The species is known only from northeastern Borneo, Malaysian states of Sabah and Sarawak.

3 Phylogeny

As BREMER (1992) already pointed out, the asymmetrical base of the aedeagus in some members of the tribe Ulomini sensu GEBIEN (1940) may be a taxonomic criterion. Apart from *Alphitobius* (8), *Diaclina* (9), *Epipedodema* (1), *Donisellus* (not seen; according to BREMER 1992), and *Guanobius* (1), the asymmetrical base of the aedeagus also exists in *Basanopsis* Gebien, 1914 (1), *Curtopeltoides* Pic, 1916 (2), *Leptoscapha* Fairmaire, 1886 (3), and *Sciophagus* Sharp, 1885 (1); the number of species studied by the author is given in parantheses. According to an unpublished diploma thesis of MEYER (see MEYER 1994), this kind of asymmetrical base of the aedeagus also occurs in *Platybolium* Blair, 1938.

The asymmetrical base of the aedeagus is most probably an apomorphic character and occurs several times in the Tenebrionidae. It is used by ARDOIN (1962) to characterize the Amarygmini Gistel, 1856, and according to a personal communication by O. MERKL (HNHM) it is characteristic for the New Guinea genus *Bothrichara* Borchmann, 1915 (Lagriini Latreille, 1825). Nevertheless, it is probable that the asymmetrical base of the aedeagus, which is protruded on the left, is an autapomorphic character of the Alphitobiini. Additional investigations are needed to prove this assumption.

According to DOYEN (1989), *Metaclisa* is placed in the tribe Alphitobiini rather than in the Tenebrionini. Own examinations of *M. viridis* (Motschulsky, 1859), *M. azurea* (Waltl, 1838), and *M. marginalis* Horn, 1870, however, found that in all three species the base of the aedeagus is characteristic indeed, but not asymmetric, and that the aedeagus is inverted. In *Metaclisa*, the base of the aedeagus narrows convergently. The phallobase is expanded and anteriorly curved. In ventral view the phallobase has the lateral borders bent inwards, therefore the base of the aedeagus looks somewhat conical. A similar structure of the aedeagus is also found in the monotypic genus *Tharsus* LeConte, 1862 (Triboliini) in which the aedeagus is similarly inverted.

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Manuscript received: 24.IX.2007, accepted: 17.X.2007.

Three new species of *Scaphidema* Redtenbacher (Coleoptera: Tenebrionidae) from China[1]

Wolfgang Schawaller

Abstract

Three new species of the genus *Scaphidema* Redtenbacher, 1849 (Coleoptera: Tenebrionidae: Scaphidemini) are described from China: *Scaphidema emeishanum* **n. sp.** from Sichuan Province, *Scaphidema shaanxicum* **n. sp.** from Shaanxi, and *Scaphidema turnai* **n. sp.** from Hubei. New synonyms and combinations: *Microbasanus* Pic, 1921 **n. syn.** of *Scaphidema* Redtenbacher, *Scaphidema khnzoriani* Kaszab, 1975 **n. syn.** of *Scaphidema jureceki* (Pic, 1921) **n. comb.** A key and remarks to all known Chinese and Korean species are included.

Keywords: Coleoptera, Tenebrionidae, *Scaphidema*, new species, China.

Zusammenfassung

Drei neue Arten der Gattung *Scaphidema* Redtenbacher, 1849 (Coleoptera: Tenebrionidae: Scaphidemini) aus China werden beschrieben: *Scaphidema emeishanum* **n. sp.** aus der Provinz Sichuan, *Scaphidema shaanxicum* **n. sp.** aus Shaanxi, und *Scaphidema turnai* **n. sp.** aus Hubei. Neue Synonyme und Kombinationen: *Microbasanus* Pic, 1921 **n. syn.** von *Scaphidema* Redtenbacher, *Scaphidema khnzoriani* Kaszab, 1975 **n. syn.** von *Scaphidema jureceki* (Pic, 1921) **n. comb.** Ein Bestimmungsschlüssel und Anmerkungen zu allen bekannten chinesischen und koreanischen Arten sind beigefügt.

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4 Key to the Chinese and Korean species of *Scaphidema* . . . 385
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1 Introduction

The genus *Scaphidema* Redtenbacher, 1849 (type species *Mycetophagus metallicus* Fabricius, 1792) as yet contains 21 species, distributed in the Holarctic Region, with the bulk of the species living in eastern Asia. Kaszab (1975) revised the Palaearctic species and Schawaller (2003) described two species from Nepal and Sichuan/China, including a general discussion of the specific characters and a check-list of all species. Subsequently, Masumoto et al. (2007) added a further species from Taiwan. Only shortly after the cited paper, I received further congeners from mainland China, described herein. The key (chapter 4) for the Chinese species includes for zoogeographical reasons also two species from adjacent Korea, described recently by Chûjô & Lee (1992, 1993), but not those from Taiwan. During a visit to the Muséum d'Histoire Naturelle de Lyon I found type material of the doubtful taxon *Microbasanus* Pic, 1921, described from the Russian Far East (see Pic 1921), which is now considered as a new junior synonym of *Scaphidema* Redtenbacher, 1849.

The shape of the aedeagus of *Scaphidema* is quite simple and similar in all species, thus not very helpful for the species identification. The dorsal colour pattern, however, is surprisingly constant and displays only minute infraspecific variability. Here we face the same situation as in the closely related genus *Basanus* Lacordaire, 1859 (Schawaller & Ando 2006). It therefore seems justified to describe new species in *Scaphidema* based on female holotypes only.

Acronyms of depositories

CJTK	Collection Jaroslav Turna, Kostelec na Hané, Czech Republic
CVTT	Collection Dr. Vladimir Tichy, Trebon, Czech Republic
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Dr. Ottó Merkl)
MHNL	Muséum d'Histoire Naturelle, Lyon, France Dr. Harold Labrique)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany

Acknowledgements

I am indebted to Jaroslav Turna (Kostelec na Hané, Czech Republic), who entrusted me with the study of several Chinese tenebrionids from his collection and who generously donated the holotypes of two of the newly described species to the SMNS. Dr. Harold Labrique (Lyon) promptly loaned upon request type

[1] Contributions to Tenebrionidae, no. 68. – For no. 67 see: Entomologica Basiliensia 29: 171–175 (2007).

material of *Microbasanus*. The hospitality of Dr. Ottó Merkl (Budapest) during my visits for comparative studies was greatly appreciated. The photographs were taken by Johannes Reibnitz (Stuttgart) with a Leica DFC320 digital camera on a Leica MZ16 APO microscope, and were then processed by him with Auto-Montage (Syncroscopy) software.

2 Descriptions of new species from China

Scaphidema emeishanum n. sp.
(Figs. 2, 7)

Holotype (♀): China, Sichuan, Emei Shan, 600–1050 m, 5.–19.V.1989, leg. L. Bocák, SMNS.

Etymology: Named after the isolated mountain Emei Shan, where the holotype was collected.

Description: Dorsal side (Fig. 2) ferrugineous with colour pattern, without any metallic shine, pronotum plain reddish, elytron with a ferrugineous posterior half and with a lighter anterior half; in the anterior half with two dark basal spots and a discal spot. Head and pronotum with large punctures of similar size, but head with distinctly denser punctuation; shape of the antennomeres see Fig. 7 (distal 3 antennomeres lacking in the holotype), antennomere 3 longer than wide, antennomere 4 short and widened. Pronotum with rough but separate punctation; anterior margin unbordered in the middle, lateral margin straight, with an apical tooth, completely bordered, the border not prolonged to the basal margin; anterior corners not protruding; propleura with a similar punctation as the disc. Elytron with 8 irregular rows of punctures without striae; these rows do not completely reach the base of the elytron; third row with about 40 punctures, which are slightly smaller than those on the pronotum; intervals flat, with scattered punctures which are smaller than those in the rows; lateral margin visible nearly along the complete length when seen from above, only hidden at the apex; epipleura without punctation. Abdominal ventrites with similar punctation as metasternum; metasternum with a short setation, abdominal ventrites without setation; last visible ventrite unbordered. Legs without peculiarities. Aedeagus unknown, only female available. Body length 3.6 mm.

Diagnosis: Characterized by a light dorsal colour pattern with a reddish pronotum, pronotum with a straight lateral margin bearing an apical tooth and with large but separate punctures, elytra with 8 irregular rows of fine punctures without striae, and widened antennomeres 4–11. Comparison to other species see identification key (chapter 4).

Scaphidema shaanxicum n. sp.
(Figs. 3, 8)

Holotype (♀): China, S Shaanxi, road Wanyuan to Zhenba, 30 km S Zhenba, 1000 m, 23.VI.2000, leg. J. Turna, SMNS.

Etymology: Named after the Chinese province Shaanxi, where the holotype was collected.

Description: Dorsal side (Fig. 3) blackish with a feeble metallic shine; elytron with a narrow, crenate, light yellow band behind the shoulders which does not reach the suture, and with a small light spot near the apex. Head with distinctly denser and coarser punctuation than pronotum; shape of the antennomeres see Fig. 8, antennomere 3 short, antennomere 4 short but not widened. Pronotum with a fine and equal punctation; anterior margin unbordered and swollen in the middle, lateral margin rounded, without any tooth, completely bordered, border not extending on the basal margin; anterior corners not protruding; propleura with punctation similar to disc. Elytron with just 6 irregular rows of punctures without striae; these rows irregularly before the base of the elytron, third row with about 45 punctures, which are similar in size to those on pronotum; intervals flat, with scattered punctures which are smaller than those on pronotal disc; lateral margin visible nearly along the complete length when seen from above, only hidden at the apex; epipleura without punctation. Abdominal ventrites with a punctation similar to the metasternum; metasternum with a short setation; abdominal ventrites without setation; the last visible ventrite unbordered. Legs without peculiarities. Aedeagus unknown, only female available. Body length 4.0 mm.

Diagnosis: Characterized by a dark dorsal colour pattern with a blackish pronotum, pronotum with a rounded lateral margin without an apical tooth and with fine and widely separate punctures, elytra with just 6 irregular rows of fine punctures without striae, and widened antennomeres 5–11. Comparison to other species see identification key (chapter 4).

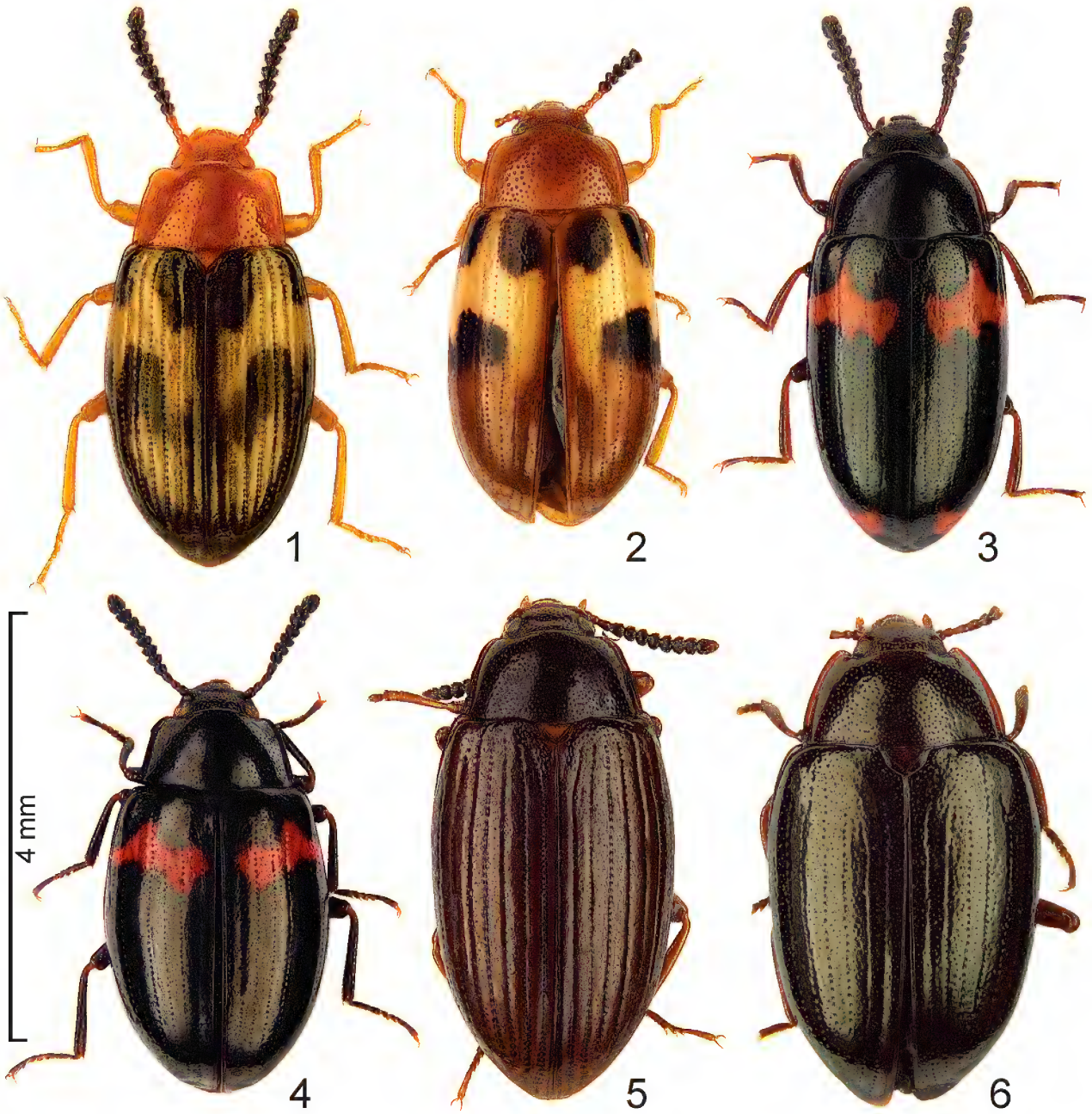
Scaphidema turnai n. sp.
(Figs. 1, 9–10)

Holotype (♂): China, W Hubei, road from Badong to Yesanguan, Tiechanghuhang, 1300 m, 27.–28.VI.2003, leg. J. Turna, SMNS.

Paratype: Same data as holotype, 1 ex. CJTK.

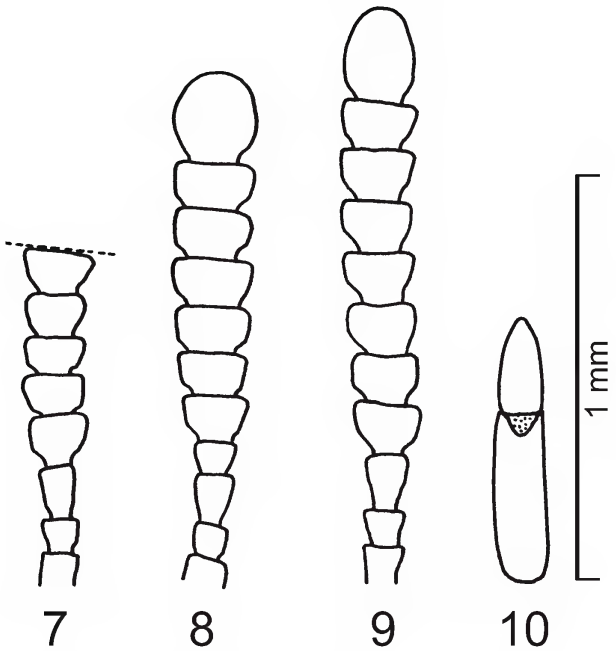
Etymology: Named in honour of Jaroslav Turna (Kostelec na Hané, Czech Republic), collector of two of the new species.

Description: Dorsal side (Fig. 1) ferrugineous with colour pattern, without any metallic shine; pronotum plain reddish; elytron dark, with an X-shaped light marking not reaching the suture. Head with distinctly denser and coarser punctuation than pronotum; shape of the antennomeres see Fig. 9, antennomere 3 short, antennomere 4 short and widened. Pronotum with a fine and equal punctation; anterior margin unbordered in the middle, lateral margin straight, with an apical tooth, com-



Figs. 1–6. Dorsal views of *Scaphidema* species. – **1**. *S. turnai* n. sp., ♂ holotype. **2**. *S. emeishanum* n. sp., ♀ holotype. **3**. *S. shaanxicum* n. sp., ♀ holotype. **4**. *S. sichuanum* Schawaller, 2003, paratype. **5**. *S. jureceki* (Pic, 1921) n. comb., paratype. **6**. *Scaphidema* sp. ♀, Sichuan.

pletely bordered, border not prolonged to the basal margin; anterior corners not protruding; propleura with a similar punctation as the disc. Elytron with 8 rows of large punctures arranged in striae, which are irregular before the base of elytron; third row with about 45 punctures, which are larger than those on the pronotum; intervals flat, with a few scattered punctures, which are distinctly smaller than those on pronotal disc; lateral margin visible nearly along the complete length when seen from above, only hidden at the apex; epipleura without punctation. Abdominal ventrites with a slightly denser punctation than on metasternum; metasternum laterally with a short setation; abdominal ventrites without setation; the last visible ventrite unbordered. Legs without peculiarities. Aedeagus see Fig. 10; joint parameres spade-like. Body length 3.8–4.0 mm.



Figs. 7–10. Antennae (7–9) and aedeagus (10) of *Scaphidema* species. – **7**. *S. emeishanum* n. sp., ♀ holotype (distal antennomeres lacking). **8**. *S. shaanxicum* n. sp., ♀ holotype. **9–10**. *S. turnai* n. sp., ♂ holotype.

Diagnosis: Characterized by a light dorsal colour pattern with reddish pronotum, pronotum with a straight lateral margin bearing an apical tooth and with fine and widely separate punctures, elytra with 8 regular rows of large punctures arranged in striae, and widened antennomeres 4–11. Comparison to other species see identification key (chapter 4).

3 Remarks to the known species from Siberia, China and Korea

Scaphidema angustatum Pic, 1935

Diagnostic characters (according to Kaszab 1975): Dorsal side plain ferrugineous or dark, without pattern. Body length: 5.0 mm.

Remarks: Doubtful taxon; neither types nor other materials were available. Shapes of antennomeres and aedeagus were not described.

Distribution: "China".

Scaphidema jureceki (Pic, 1921) **n. comb.**
(Fig. 5)

Microbasanus jureceki Pic, 1921.
Scaphidema khnzoriani Kaszab, 1975 **n. syn.**

Material: Eastern Siberia (labelled as Ussuri med.), Vladivostok, 1919, leg. Jureček, 2 paratypes of *Microbasanus jureceki* MHNL. – Eastern Siberia, Ussuri, Schkotovo, 12.VIII.1971, leg. M. Khnzorian, 1 paratype of *Scaphidema khnzoriani* HNHM. – Eastern Siberia (labelled as S Primorje), Vladivostok, 20.VIII.1986, leg. T. Kompantzeva, 1 ex. SMNS (*Scaphidema khnzoriani* det. Kompantzeva).

Synonymy: The paratypes of *Microbasanus jureceki* and *Scaphidema khnzoriani* which were examined show no generic or specific differences; therefore *Microbasanus* Pic, 1921 is a junior synonym of *Scaphidema* Redtenbacher, 1849, and *Scaphidema khnzoriani* Kaszab, 1975 is a junior synonym of *Scaphidema jureceki* (Pic, 1921) n. comb.

Distribution: Eastern Siberia (Primorje Region).

Scaphidema kayokoae Chûjô, 1992

Diagnostic characters: Dorsal side with colour pattern: Elytron with a wide transverse band not reaching the suture, and with a spot near the apex. Elytron with 8 rows of deep and large punctures arranged in striae. Lateral margin of pronotum straight, with an apical tooth. Antennomere 3 long; antennomere 4 short, not widened. Body length: 3.7–4.7 mm.

Remarks: Characters are taken from the original figures in Chûjô & Lee (1992); aedeagus unknown. The author of the species is only M. T. Chûjô.

Distribution: S Korea (Chejudo Island).

Scaphidema michihidei Chûjô & Lee, 1993

Diagnostic characters: Dorsal side dark ferrugineous, without pattern. Elytron with 8 rows of deep and large punctures arranged in striae. Lateral margin of pronotum straight, with an apical tooth. Antennomere 3 long; antennomere 4 short, widened. Body length: 4.65–4.90 mm.

Remarks: Characters are taken from the original figures in Chûjô & Lee 1993; aedeagus unknown. This species may be a junior synonym of *Scaphidema angustatum* Pic, 1935, which was described from "China".

Distribution: S Korea.

Scaphidema sp.
(Fig. 6)

Material: China, Central Sichuan, Volong, 150 km SW Chengdu, 9.–10.VII.1994, leg. V. Beneš, 1 ♀ CVTT.

Remarks: This specimen may belong to *Scaphidema angustatum* or represent another new species from China. Because of the uncertain taxonomic position I refrain from describing it until more material will be available. This female represents a monochromatic metallic species without an apical tooth at the lateral margin of the pronotum and is similar to the European species *Scaphi-*

dema metallicum (Fabricius, 1792). However, in the Chinese species the pronotal margin is more rounded, and the elytral intervals are more densely punctured.

4 Key to the Chinese and Korean species of *Scaphidema*

1 Dorsal side plain ferrugineous or blackish, without any colour pattern; body length 4.65–5.00 mm (two or even three species, separation doubtful). **2**
– Dorsal side with a light or dark colour pattern; body length 3.3–4.0 mm. **3**
2 Species from "China". . . . . ***angustatum***
– Species from S Korea. . . . . ***michihidei***
3 Lateral margin of pronotum rounded, without an apical tooth; dorsal colour pattern of elytra dark (Fig. 3); aedeagus unknown. . . . . ***shaanxicum* n. sp.**
– Lateral margin of pronotum straight, with an apical tooth. **4**
4 Punctures of elytral rows fine, not arranged in striae. **5**
– Punctures of elytral rows large, arranged in striae. **6**
5 Elytron mostly light. Pronotum reddish, with large but separate punctures (Fig. 2); aedeagus unknown. . . . . ***emeishanum* n. sp.**
– Elytron mostly dark. Pronotum dark (Fig. 4), with fine and widely separate punctures; aedeagus see SCHAWALLER (2003: fig. 9). . . . . ***sichuanum***
6 Elytron with a wide transverse band and with or without an apical spot, pronotum dark ferrugineous (see CHÛJÔ & LEE 1992: fig. 5); aedeagus unknown. – Insular species (Korea/Chejudo Island). . . . . ***kayokoae***
– Elytron with a quite different, X-like colour pattern, pronotum reddish (Fig. 1); aedeagus see Fig. 10. – Continental species (Hubei). . . . . ***turnai* n. sp.**

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Manuscript received: 26.II.2007, accepted: 18.VI.2007.

The genus *Laena* Latreille (Coleoptera: Tenebrionidae) in China (part 2), with descriptions of 30 new species and a new identification key[1]

Wolfgang Schawaller

Abstract

New species of the genus *Laena* Latreille, 1829 (Coleoptera: Tenebrionidae) from China are described and newly collected specimens of previously known species are recorded. The distribution range of newly treated specimens also includes those Chinese provinces (Fujian, Guangxi, Guizhou, Henan, Jiangxi) from where previously no species of *Laena* were known. Five species are transferred from the genus *Laena* to the genus *Hypolaenopsis* Masumoto, 2001. New identification keys for all known species of *Laena* (96) and *Hypolaenopsis* (5) from China including Tibet are compiled. – New species: *Laena alesi* **n. sp.** (Yunnan), *L. baiorum* **n. sp.** (Yunnan), *L. baoshanica* **n. sp.** (Yunnan), *L. barkamica* **n. sp.** (Sichuan), *L. basumtsoica* **n. sp.** (Tibet), *L. bohrni* **n. sp.** (Sichuan), *L. cooteri* **n. sp.** (Jiangxi, Fujian), *L. dabashanica* **n. sp.** (Hubei), *L. davidi* **n. sp.** (Sichuan), *L. farkaci* **n. sp.** (Yunnan), *L. fouquei* **n. sp.** (Yunnan), *L. gaoligongica* **n. sp.** (Yunnan), *L. guangxica* **n. sp.** (Guangxi), *L. guizhouica* **n. sp.** (Guizhou), *L. gyalthangica* **n. sp.** (Yunnan), *L. hlavaci* **n. sp.** (Jiangxi), *L. janatai* **n. sp.** (Sichuan), *L. jiangxica* **n. sp.** (Jiangxi), *L. jinpingica* **n. sp.** (Sichuan), *L. kalabi* **n. sp.** (Sichuan), *L. lisuorum* **n. sp.** (Yunnan), *L. maowenica* **n. sp.** (Sichuan), *L. michaeli* **n. sp.** (Yunnan), *L. moxica* **n. sp.** (Sichuan), *L. naxiorum* **n. sp.** (Yunnan), *L. nujiangica* **n. sp.** (Yunnan), *L. quinquagesima* **n. sp.** (Yunnan), *L. sehnali* **n. sp.** (Sichuan), *L. septuagesima* **n. sp.** (Yunnan), *L. xueshanica* **n. sp.** (Yunnan). – New combinations: *Hypolaenopsis benesi* (Schawaller, 2001) **n. comb.**, *H. hongyuanica* (Schawaller, 2001) **n. comb.**, *H. hualongica* (Schawaller, 2001) **n. comb.**, *H. nanpingica* (Schawaller, 2001) **n. comb.**, *H. nomurai* (Schawaller, 2001) **n. comb.**, all from *Laena*. – New synonym by priority: *Hypolaenopsis nanpingica* (Schawaller, 2001) = *H. uenoi* Masumoto, 2001 **n. syn.**

Keywords: Coleoptera, Tenebrionidae, *Laena*, *Hypolaenopsis*, China, new species, taxonomy, distribution, identification key.

Zusammenfassung

Neue Arten der Gattung *Laena* Latreille, 1829 (Coleoptera: Tenebrionidae) aus China werden beschrieben und neu gesammelte Exemplare bekannter Arten werden aufgeführt. Die neu behandelten Exemplare stammen auch aus solchen chinesischen Provinzen (Fujian, Guangxi, Guizhou, Henan, Jiangxi), aus denen bislang keine *Laena*-Arten bekannt waren. Fünf Arten werden von der Gattung *Laena* zur Gattung *Hypolaenopsis* Masumoto, 2001 verschoben. Neue Bestimmungsschlüssel für alle bekannten Arten von *Laena* (96) und *Hypolaenopsis* (5) aus Xhina einschließlich Tibet werden erstellt. – Neue Arten: *Laena alesi* **n. sp.** (Yunnan), *L. baiorum* **n. sp.** (Yunnan), *L. baoshanica* **n. sp.** (Yunnan), *L. barkamica* **n. sp.** (Sichuan), *L. basumtsoica* **n. sp.** (Tibet), *L. bohrni* **n. sp.** (Sichuan), *L. cooteri* **n. sp.** (Jiangxi, Fujian), *L. dabashanica* **n. sp.** (Hubei), *L. davidi* **n. sp.** (Sichuan), *L. farkaci* **n. sp.** (Yunnan), *L. fouquei* **n. sp.** (Yunnan), *L. gaoligongica* **n. sp.** (Yunnan), *L. guangxica* **n. sp.** (Guangxi), *L. guizhouica* **n. sp.** (Guizhou), *L. gyalthangica* **n. sp.** (Yunnan), *L. hlavaci* **n. sp.** (Jiangxi), *L. janatai* **n. sp.** (Sichuan), *L. jiangxica* **n. sp.** (Jiangxi), *L. jinpingica* **n. sp.** (Sichuan), *L. kalabi* **n. sp.** (Sichuan), *L. lisuorum* **n. sp.** (Yunnan), *L. maowenica* **n. sp.** (Sichuan), *L. michaeli* **n. sp.** (Yunnan), *L. moxica* **n. sp.** (Sichuan), *L. naxiorum* **n. sp.** (Yunnan), *L. nujiangica* **n. sp.** (Yunnan), *L. quinquagesima* **n. sp.** (Yunnan), *L. sehnali* **n. sp.** (Sichuan), *L. septuagesima* **n. sp.** (Yunnan), *L. xueshanica* **n. sp.** (Yunnan). – Neue Kombinationen: *Hypolaenopsis benesi* (Schawaller, 2001) **n. comb.**, *H. hongyuanica* (Schawaller, 2001) **n. comb.**, *H. hualongica* (Schawaller, 2001) **n. comb.**, *H. nanpingica* (Schawaller, 2001) **n. comb.**, *H. nomurai* (Schawaller, 2001) **n. comb.**, alle von *Laena*. – Neues Synonym wegen Priorität: *Hypolaenopsis nanpingica* (Schawaller, 2001) = *H. uenoi* Masumoto, 2001 **n. syn.**

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[1] Contributions to Tenebrionidae, no. 69. – For no. 68 see Stuttgarter Beiträge zur Naturkunde A, N. S. 1: 381–385 (2008).

1 Introduction

After publishing the recent revision of the Chinese *Laena* (SCHAWALLER 2001), I was immediately provided with a considerable number of newly collected specimens of this genus from different Chinese localities. These specimens turned out to be either new faunistic records, or again numerous new taxa, listed and described herein. The distribution range of newly treated specimens also includes those Chinese provinces (Fujian, Guangxi, Guizhou, Henan, Jiangxi) from where previously no species of *Laena* were known; nearly all those taxa are new to science. China houses an incredibly high number of species (96 at present) of the tenebrionid genus *Laena*. All species are wingless and nearly all species have restricted distribution areas. It can be predicted, that every subsequent finding in an as yet "unsifted" mature mountainous forest will yield further new taxa. The older references concerning the Chinese fauna are listed in my first contribution and are not repeated here. In additional recent papers our knowledge upon the genus *Laena* in the Nepal Himalayas (SCHAWALLER 2002) and in adjacent continental southeastern Asia except China (SCHAWALLER 2006) is summarized.

Through the courtesy of I. LÖBL (in litt.) I recently became aware of a hidden paper of JINGKE & PENG (1993), in which a new species of *Laena* from the Anhui Province is described. This description consists only of a few lines in Chinese, without any figures or a diagnosis, thus the taxonomic status of this taxon remains unclear. Moreover, the species name *chinensis* is a homonym of *Laena chinensis* Kaszab, 1965. A replacement name for *chinensis* Jingke & Peng will be chosen in a forthcoming paper together with I. LÖBL.

Concerning the species characters within the genus *Laena* I refer to the cited papers. As stated earlier, some taxa in this species-rich genus form natural groups (e. g. those species transferred herein to the genus *Hypolaenopsis* Masumoto, 2001, see chapter 2 below), but the bulk of the species still represents an unsatisfactory assemblage without resolved phylogenetic structure.

Acronyms of depositories

BMNH	The Natural History Museum, London (MAX BARCLAY)
CAPE	Collection ANDREAS PÜTZ, Eisenhüttenstadt
CASO	Collection Dr. ALEŠ SMETANA, Ottawa
CHHR	Collection HANS HEBAUER, Rain
CJTK	Collection JAROSLAV TURNA, Kostelec na Hané
CKBB	Collection KAROL BOHRN, Bratislava
CLSM	Collection LAURENT SOLDATI, Montferrier
CMLS	Collection MARTIN LILLIG, Saarbrücken
CRFL	Collection RENÉ FOUQUÈ, Liberec
CRSW	Collection RUDOLF SCHUH, Wien
CSBC	Collection STANISLAV BEČVÁŘ, České Budějovice
DEI	Deutsches Entomologisches Institut, Münchefeld (Dr. LOTHAR ZERCHE)
HNHM	Hungarian Natural History Museum, Budapest (Dr. OTTÓ MERKL)
NHMB	Naturhistorisches Museum, Basel (Dr. MICHEL BRANCUCCI)
NHMW	Naturhistorisches Museum, Wien (Dr. HARALD SCHILLHAMMER)
OUMNH	HOPE Entomological Collections, Oxford University Museum of Natural History (JON COOTER)
SMNS	Staatliches Museum für Naturkunde, Stuttgart

Acknowledgements

I would like to thank all friends and colleagues, as listed in the list of depositories, who entrusted me again with the study of specimens of *Laena* housed in the collections under their care. My particular thanks go to JON COOTER (Hereford), ROBERTO FABBRI (Lavezzola/Ravenna), MICHAEL SCHÜLKE (Berlin), Dr. ALEŠ SMETANA (Ottawa), LAURENT SOLDATI (Monferrier), JAROSLAV TURNA (Kostelec na Hané) and DAVID WRASE (Berlin), who generously allowed me to keep at least parts of their collections in Stuttgart. The hospitality during my visits for comparative studies in Budapest (Dr. OTTÓ MERKL) and Basel (Dr. EVA SPRECHER) is greatly appreciated. JOHANNES REIBNITZ (Stuttgart) scanned my drawings and combined them on plates. Last but not least I thank Dr. ROLAND GRIMM (Tübingen) and Dr. OTTÓ MERKL (Budapest) as referees for their corrections and comments.

2 Species of *Hypolaenopsis*

MASUMOTO (December 30, 2001) described the genus *Hypolaenopsis* erroneously within the tribe Adeliini (and not in Laenini), based on the single species *H. uenoi*. Nearly simultaneously, SCHAWALLER (November 30, 2001) published the first contribution on the Chinese species of *Laena*, describing five new species from that group. In that paper, I gave arguments that these five species form a natural group, but that this group is still included in *Laena* as long as a complete phylogenetic classification of this species-rich genus is not available. Due to MASUMOTO's description, these five species are here formally transferred to *Hypolaenopsis*, although its phylogenetic position within the *Laena*-complex is still unsolved.

Hypolaenopsis benesi (Schawaller, 2001) **n. comb.**

New material: Sichuan, Ganzi Tibetian Autonomous Prefecture, 55 km NE Batang, Shaluli Shan, 4200 m, 3.VII.1999, leg. A. PÜTZ, 2 ex. CAPE.

New combination: See remarks on genus *Hypolaenopsis*.

Hypolaenopsis hongyuanica (Schawaller, 2001) **n. comb.**

New material: NW Sichuan, between Luhuo and Sanggarmai, pass W Luhuo, 4200–4300 m, 8.–28.VI.2004, leg. R. FABBRI, 4 ex. SMNS. – W Sichuan, pass SE Barkam, pass between Zhuokeji and Lianghekou, 4100 m, 10.–30.VI.2004, leg. R. FABBRI, 1 ex. SMNS. – W Sichuan, road Luhuo to Sertar, pass 40 km N Luhuo, 4200 m, 22.VII.1997, leg. M. TRÝZNA & O. ŠAFRANEK, 2 ex. CJTK.

New combination: See remarks on genus *Hypolaenopsis*.

Hypolaenopsis hualongica (Schawaller, 2001) **n. comb.**

New material: NW Sichuan, 20 km S Maeirma, 3800 m, 9.–29.VI.2004, leg. R. Fabbri, 2 ex. SMNS. – Central Sichuan, N pass Zhangla, Nanping, 4000 m, 22.VI.1996, leg. M. Janata, 13 ex. CKBB, 2 ex. SMNS. – N Sichuan, 60 km S Hongyan, 2400 m, 27.–29.VI.1991, leg. J. Kaláb, 2 ex. CKBB, 2 ex. SMNS.

New combination: See remarks on genus *Hypolaenopsis*.

Hypolaenopsis nanpingica (Schawaller, 2001) **n. comb.**

Hypolaenopsis uenoi Masumoto, 2001 **n. syn.**

New combination: See remarks on genus *Hypolaenopsis*.

New synonymy: Both described taxa are conspecific, the species synonymy is caused by priority: Masumoto (December 30, 2001), Schawaller (November 30, 2001).

Hypolaenopsis nomurai (Schawaller, 2001) **n. comb.**

New material: NW Sichuan, Min Shan, 2500–4500 m, 14.–16.VII.1990, leg. J. Kolíbáč, 1 ♂ SMNS.

New combination: See remarks on genus *Hypolaenopsis*.

Remarks: The identification of the newly listed specimen is uncertain, because the pronotum is somewhat longer as in the type series. However, the aedeagus shows no distinct differences.

3 Key to the species of *Hypolaenopsis* in China

Also compare figures of the specific characters in Schawaller (2001), cited in the present new key as "Sch: figs.".

1 Pronotum with crenulated lateral margins. – Sch: figs. 2–5. . . . . ***nomurai***
– Pronotum with smooth lateral margins. **2**
2 Prontum wider than medially long, maximum width near base. – Sch: figs. 6–9. . . . . ***hualongica***
– Pronotum subquadrate or longer than wide, maximum width at or anterior to the middle. **3**
3 Pronotum with the maximum width near the middle, apicale very short, triangular. – Sch: figs. 10–13. . . . . ***hongyuanica***
– Pronotum with the maximum width in the anterior part, apicale very long, finger-like or shape unknown. **4**
4 Eyes completely reduced, only with some lighter cuticular spots; pronotum trapezoid, with straight lateral margins; aedeagus unknown. – Sch: figs. 14–16. . . . . ***nanpingica***
– Eyes not completely reduced, kidney-shaped in lateral view; pronotum cordiform, with rounded lateral margins; aedeagus with long, finger-like apicale. – Sch: figs. 17–20. ***benesi***

4 New species of *Laena*

Laena alesi **n. sp.**
(Figs. 97–100)

Holotype (♂): China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. A. Smetana, SMNS.

Paratypes: China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. M. Schülke, 3 ex. SMNS.

Etymology: Named in honour of Dr. Aleš Smetana (Ottawa), who collected several species of *Laena* in China and generously deposited most of them in the Natural History Museum Stuttgart.

Description: Body length 6.2–6.5 mm. Eyes (Fig. 97) not reduced, not prominent. Shape of pronotum see Fig. 97, disc with scattered punctures slightly varying in size, distance between 0.5–5 diameters, all punctures bearing short adpressed setae, surface with a pair of feeble impressions and slightly shagreened, lateral margins bordered and before the middle with a distinct irregular emargination, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation than on disc and without setation. Elytra (Fig. 97) with rows of punctures without striae, punctures of rows of similar size as pronotal punctures, each puncture bearing a microseta, intervals with very few nearly indistinct punctures bearing a short and adpressed seta, all intervals flat and shining, interval 9 with 4 indistinct setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 98–99). Aedeagus see Fig. 100.

Diagnosis: With *Laena xueshanica* n. sp. from Yunnan *L. alesi* n. sp. shares the general body size and shape, the general dorsal punctation and setation, and the laterally bordered pronotum. *L. alesi* n. sp can be recognized by a distinct irregular emargination before the middle of the pronotal lateral margins, by larger punctures in the elytral rows, by unmodified male tibiae, and by a different aedeagus with acute apicale (blunt tip in *L. xueshanica* n. sp.). *L. naxiorum* n. sp., also from Yunnan, belongs to the same group of species, but has a different shape of the pronotum without lateral emargination, modified male tibiae, and also a different aedeagus.

Laena baiorum **n. sp.**
(Figs. 101–104)

Holotype (♂): China, N Yunnan, Diancang Shan 5 km SSW Dali, 2800 m, 26.VIII.2003, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 4 ex. SMNS. – China, N Yunnan, Diancang Shan 5 km SSW Dali, 2800 m, 26.VIII.2003, leg. D. Wrase, 1 ex. CJTK. – China, N Yunnan, Diancang Shan 3 km W Dali, 2700 m, 28.VIII.2003, leg. D. Wrase, 1 ex. CJTK.

Etymology: Named in honour of the Chinese minority Bai mainly settling in the village Dali, in whose adjacent Diancang Shan the type series was collected.

Description: Body length 8.0–9.0 mm. Eyes (Fig. 101) not reduced, prominent. Shape of pronotum see Fig. 101, disc with coarse but not confluent punctures, distance between 0.5–1 diameters, most punctures bear-

ing short adpressed setae; surface uneven, with a pair of impressions on the disc and with an indistinct mediobasal impression, surface somewhat shagreened but shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 101) with rows of punctures without striae, these rows disappearing in the posterior part, punctures of rows slightly smaller than pronotal punctures, each puncture bearing a microseta, intervals with very few indistinct punctures bearing a similar small adpressed seta, intervals 1–6 flat, external intervals convex, interval 9 with 2 distinct setiferous pores. All femora in both sexes without teeth. Posterior tibiae of males basomedially somewhat swollen (Figs. 102–103). Aedeagus see Fig. 104.

Diagnosis: *Laena baiorum* n. sp. and *L. fouquei* n. sp. share the medium-sized body length, the prominent eyes, the laterally bordered pronotum with a pair of discal impressions, the dorsal punctation and very short dorsal setation, and also the shape of the aedeagus. In *L. fouquei* n. sp., however, the shape of the pronotum is different, widest in the middle (widest in the anterior part in *L. baiorum* n. sp.), the pronotal punctation is somewhat finer and the posterior male tibiae are unmodified. *L. yufengsi* Masumoto, 1996, also from Yunnan, belongs to the same group, but in this species the pronotum shape is also different and its lateral margins are indistinctly bordered, the aedeagus is different and the male posterior tibiae are without modification.

Laena baoshanica **n. sp.**
(Figs. 113–116)

Holotype (♂): China, Yunnan, Gaoligong Shan, pass SW Baoshan, 4.–8.VI.2005, leg. I. Jeniš, CJTK.

Paratypes: Same data as holotype, 4 ex. CJTK, 3 ex. SMNS.

Etymology: Named after the village Baoshan, where the types were collected.

Description: Body length 4.8–6.0 mm. Eyes (Fig. 113) not reduced, prominent. Shape of pronotum see Fig. 113, disc scattered with large punctures, distance between 0.5–2 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation than but similar long setation as on disc. Elytra (Fig. 113) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with a row of fine punctures bearing a similar long seta, all intervals flat and shining, interval 9 with 4 distinct setiferous pores. All femora in both sexes without teeth. Posterior tibiae of males medially swollen and interiorly with hooked apex (Figs. 114–115). Aedeagus see Fig. 116.

Diagnosis: *Laena baoshanica* n. sp. can be recognized by the prominent eyes, the bordered lateral margins of the pronotum, the long and erect dorsal setation, the unarmed femora and the medially swollen posterior tibiae in males, and the shape of the aedeagus. The prominent eyes are quite unusual among the nearly 100 Chinese species; only *L. angulifemoralis* Masumoto, 1996, also from Yunnan, has similar eyes (also a similar shape of the pronotum with lateral border, and a long dorsal setation), but in that species all femora are armed by distinct angles, and the shape of the aedeagus is different.

Laena barkamica **n. sp.**
(Figs. 69–72)

Holotype (♂): China, W Sichuan, Qionglai Shan, Mou Pi Shan, Barkam, 15 km S Zhuokeji, 3100–3750 m, 10.–30. VI.2004, leg. R. Fabbri, SMNS.

Paratypes: Same data as holotype, 10 ex. SMNS, 2 ex. HNHM.

Etymology: Named after the village Barkam, where the types were collected.

Description: Body length 3.8–5.0 mm. Eyes (Fig. 69) not reduced, not prominent. Shape of pronotum see Fig. 69, disc scattered with large punctures, distance between 2–3 diameters, all punctures bearing small adpressed setae, surface without impressions and shining, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation than and similar setation as on disc. Elytra (Fig. 69) with rows of punctures without striae, punctures of rows smaller than punctures on pronotum, each puncture bearing a short and adpressed seta, intervals with very few nearly indistinct punctures bearing a similar short seta, all intervals flat and shining, interval 9 with 3 setiferous pores. All femora in both sexes with teeth. All tibiae of males without modifications (Figs. 70–71). Aedeagus see Fig. 72.

Diagnosis: *Laena barkamica* n. sp. and *L. fengileana* Masumoto, 1996 from Shaanxi and Sichuan share the general body size and shape, the unbordered lateral margins of the pronotum and the armed femora, but *L. barkamica* n. sp. can be separated by larger and denser setation on the pronotum, short and adpressed dorsal setation on pronotum and elytra, smaller elytral punctures, and different shape of the aedeagus.

Laena basumtsoica **n. sp.**
(Figs. 25–28)

Holotype (♂): China, E Tibet, 90 km W Gyamda, Basum Tso, 3700 m, 17.VI.2001, leg. A. Wrzecionko, CJTK.

Paratypes: Same data as holotype, 2 ex. CJTK, 1 ex. SMNS.

Etymology: Named after the region and lake Basum Tso, where the type series was collected.

Description: Body length 7.5–8.5 mm. Eyes (Fig. 25) not reduced, not prominent. Shape of pronotum see Fig. 25, disc with dense but not confluent punctures, distance between 1–3 diameters, all punctures bearing longer adpressed setae, surface with a pair of feeble impressions on the disc and a feeble mediobasal impression, and shagreened, lateral margins finely bordered, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with sparser punctation and shorter setation than on disc. Elytra (Fig. 25) with rows of punctures without striae; these rows partly disappearing in posterior part, punctures of rows as large as pronotal punctures, most punctures bearing a microseta, intervals with a few scattered fine punctures which are smaller than the punctures of the rows bearing a similar microseta; internal intervals flat and feebly shagreened, interval 9 with 3 indistinct setiferous pores. All femora in both sexes without teeth. All tibiae of males interiorly with a few granules (Figs. 26–27). Aedeagus see Fig. 28.

Diagnosis: With *Laena janatai* n. sp. from Sichuan *L. basumtsoica* n. sp. shares the general body size and shape, as well as the pronotum with protruding anterior corners and bordered lateral margins; however, in *L. janatai* n. sp. the pronotal punctation is distinctly coarser, the elytral intervals are distinctly punctate, the elytral interval 7 is somewhat convex, the male tibiae show no distinct modifications, and the parameres of the aedeagus are somewhat broader. *L. michaeli* n. sp. and *L. quinquagesima* n. sp., both from Yunnan, have a similarly shaped pronotum, but both have a different dorsal punctation, a laterally unbordered or incompletely bordered pronotum, and a different shape of the aedeagus, besides other characters.

Laena bohrni **n. sp.**
(Figs. 53–56)

Holotype (♂): China, W Sichuan, S Barkam, between Lianghekou and Fubian, 3450–3650 m, 10.–30.VI.2004, leg. R. Fabbri, SMNS.

Paratypes: China, N Sichuan, valley SW Barkam, 3000–3800 m, 22.VII.1995, leg. M. Janata, 4 ex. CKBB, 1 ex. SMNS.

Etymology: Named in honour of Karol Bohrn (Bratislava), who entrusted me with the study of specimens from his collection and who allowed me to keep some duplicates.

Description: Body length 7.5–8.5 mm. Eyes (Fig. 53) not reduced, not prominent. Shape of pronotum see Fig. 53, disc with coarse and partly confluent punctures, distance between 0.5–2 diameters, most punctures bearing short adpressed setae; surface uneven, with a pair of indistinct impressions on the disc and with an indistinct longitudinal medial impression, surface shining, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with larger but sparser punctation than and similar setation as on disc. Elytra (Fig. 53) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a small and adpressed seta, intervals with a few very fine punctures bearing a similar seta, intervals flat, intervals 5 and 7 slightly convex but not keel-like, intervals 3, 5 and 7 somewhat broader and even darker than other intervals, interval 9 with 4 distinct setiferous pores. All femora in both sexes with strong teeth, teeth of anterior femur with blunt tip. All tibiae of males without modifications (Figs. 54–55). Aedeagus see Fig. 56.

Diagnosis: *Laena bohrni* n. sp. can be recognized by its large body size, by its distinctly armed femora, by its round and convex pronotum with coarse punctation without lateral border, and by the shape of its aedeagus. *L. ganzica* Schawaller, 2001 from Sichuan is similar and has even a similar shape of the aedeagus, but that species is smaller (6.0–7.2 mm), the pronotum is longer and the elytral intervals 3, 5 and 7 are distinctly convex. *L. smetanai* Schawaller, 2001, also from Sichuan, belongs to the same group, has a similarly round and convex pronotum, but its pronotal punctation is much finer and sparser and its aedeagus is different. See also under *L. dabashanica* n. sp. from Hubei.

Laena cooteri **n. sp.**
(Figs. 5–8)

Holotype (♂): China, Jiangxi, Wuyi Shan Nature Reserve, Huanggan Shan, 1800–2050 m, 5.VI.2001, leg. J. Cooter & P. Hlaváč, SMNS.

Paratypes: Same data as holotype, 3 ex. HNHM. – China, W Fujian, Emei Feng, 1555 m, 24.IV.2006, leg. J. Turna, 1 ex. CJTK.

Etymology: Named in honour of Jon Cooter (Hereford, England), one of the collectors of the type series.

Description: Body length 4.0–5.2 mm. Eyes (Fig. 5) not reduced, not prominent. Shape of pronotum see Fig. 5, disc scattered with large punctures, distance between 2–5 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation than and similar setation as on disc. Elytra (Fig. 5) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals slightly convex and shining, interval 9 with 4 indistinct setiferous pores. All femora in both sexes with a pair of unequal teeth, in the anterior and middle femora the pair consists of a prominent and a tubercle-like tooth, on the posterior femora the pair con-

sists of a longer and a shorter tooth. All tibiae of males without modifications (Figs. 6–7). Aedeagus see Fig. 8.

Diagnosis: The three species newly described herein from Province Jiangxi (*Laena cooteri* n. sp., *L. hlavaci* n. sp., *L. jiangxica* n. sp.) share the general body size and shape and the dorsal punctation and setation, but can be separated by the unarmed (*L. jiangxica* n. sp.) or armed femora (*L. cooteri* n. sp., *L. hlavaci* n. sp.), by unbordered (*L. hlavaci* n. sp.) or bordered lateral margins of the pronotum (*L. cooteri* n. sp., *L. jiangxica* n. sp.), by shagreened (*L. hlavaci* n. sp.) or shining pronotal surface (*L. cooteri* n. sp., *L. jiangxica* n. sp.), by flat (*L. hlavaci* n. sp.) or slightly convex elytral intervals (*L. cooteri* n. sp., *L. jiangxica* n. sp.), and by a different shape of the aedeagus. See also under *L. jiangxica* n. sp. concerning the separation of *L. guizhouica* n. sp. from Province Guizhou.

Distribution: The type locality in the Province Jiangxi is situated close to the adjacent locality in Fujian, which is in the same mountain range.

Laena dabashanica **n. sp.**
(Figs. 37–40)

Holotype (♂): China, W Hubei, Daba Shan, pass E Mt. Da Shennongjia, 12 km NW Muyuping, 1950 m, 16.–22.VII.2001, leg. D. Wrase, SMNS.

Paratypes: Hubei, Daba Shan, 13 km NW Muyuping, 1900 m, 16.VII.2002, leg. Stary, 1 ex. CRSW, 1 ex. SMNS. – W Hubei, Daba Shan, pass E Mt. Da Shennongjia, 12 km NW Muyuping, 1950 m, 16.–22.VII.2001, leg. A. Smetana, 1 ex. CASO, 1 ex. SMNS. – W Hubei, Daba Shan, 11 km NW Muyuping, 1960 m, 18.VII.2001, leg. A. Smetana, 1 ex. SMNS.

Etymology: Named after the Daba Shan [Shan = Mountain], where the types were collected.

Description: Body length 7.5–8.5 mm. Eyes (Fig. 37) not reduced, not prominent. Shape of pronotum see Fig. 37, disc with coarse and partly confluent punctures, distance between 0.5–3 diameters, most punctures bearing short adpressed setae; surface uneven, with a pair of distinct impressions on the disc and with an indistinct mediobasal impression, surface shining, lateral margins indistinctly bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with slightly wider punctation than and similar setation as on disc. Elytra (Fig. 37) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a small and adpressed seta, intervals with a few very fine punctures bearing a somewhat longer seta, internal intervals flat, interval 7 distinctly convex and nearly keel-like except at the elytral tip, interval 9 with indistinct setiferous pores. All femora in both sexes with strong teeth, teeth of anterior femur with blunt tip. All tibiae of males without modifications (Figs. 38–39). Aedeagus see Fig. 40.

Diagnosis: *Laena dabashanica* n. sp. and *L. chinensis* Kaszab, 1965 share the general body size and shape, the shining dorsal surface and elytral punctation, and the strong femoral teeth, but the new species can be distinguished by a denser pronotal punctation, indistinct pronotal lateral margins, a strongly convex elytral interval 7, and a different shape of the aedeagus.

Laena davidi **n. sp.**
(Figs. 77–80)

Holotype (♂): China, W Sichuan, Daxue Shan, E Tsheto La pass, W Kangding, 3500 m, 25.V.1997, leg. D. Wrase, SMNS.

Paratype: China, NW Sichuan, Maeirma, 40 km SE Aba, 3250 m, 9.–29.VI.2004, leg. R. Fabbri, 1 ex. SMNS.

Etymology: Named in honour of David Wrase (Berlin), who collected the holotype and several other species of *Laena* in China and generously deposited most of them in the Natural History Museum Stuttgart.

Description: Body length 4.2–4.7 mm. Eyes (Fig. 77) not reduced, not prominent. Shape of pronotum see Fig. 77, disc with coarse and confluent punctures, distance between 0.5–1 diameters, most punctures bearing short adpressed setae; surface uneven, with a pair of deep impressions and a medial longitudinal impression on the disc and with a laterobasal impression besides the posterior angles, surface dull, lateral margins distinctly marked and crenulate but unbordered, basal margin unbordered and not bent downwards, posterior angles slightly marked, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 77) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a small and adpressed seta, intervals with similar small adpressed seta, intervals 3, 5 and 7 distinctly convex but not keel-like, the other intervals flat, interval 9 without distinct setiferous pores. All femora in males (female unknown) without teeth. Posterior tibiae of males with finely hooked inner apex (Figs. 78–79). Aedeagus see Fig. 80.

Diagnosis: With *Laena luhuoica* Schawaller, 2001 from Sichuan *L. davidi* n. sp. shares the small body size and shape, the dull surface, the coarse punctation and the impressions on the pronotum, the unarmed femora and the male posterior tibiae with finely hooked inner apex, and even the shape of the aedeagus. However, in *L. davidi* n. sp. the elytra bear distinct and equally convex intervals 3, 5 and 7, and the joint elytral disc between the intervals 7 is nearly flat, whereas in *L. luhuoica* only the interval 7 is marked and the disc between the intervals 7 is convex. Additionally, the pronotum is flatter in *L. davidi* n. sp.

Laena farkaci **n. sp.**
(Figs. 61–64)

Holotype (♂): China, N Yunnan, Xue Shan near Zhongdian, 3800 m, 26.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, NHMB.

Paratypes: Same data as holotype, 8 ex. NHMB, 5 ex. SMNS. – N Yunnan, 51 km SSE Zhongdian, 2970 m,

16.VIII.2003, leg. A. Smetana, 3 ex. CASO. – N Yunnan, 46 km SSE Zhongdian, 3050–3100 m, 17.VIII.2003, leg. A. Smetana, 6 ex. SMNS. – N Yunnan, 46 km SSE Zhongdian, 3050–3100 m, 17.VIII.2003, leg. D. Wrase, 5 ex. CJTK. – N Yunnan, 48 km N Zhongdian, 3220 m, 21.VIII.2003, leg. A. Smetana, 3 ex. SMNS. – N Yunnan, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. A. Smetana, 4 ex. SMNS, 3 ex. HNHM.

Etymology: Named in honour of Dr. Jan Farkač (Prague), one of the collectors of the type series.

Description: Body length 3.5–4.3 mm. Eyes (Fig. 61) not reduced, not prominent. Shape of pronotum see Fig. 61, disc with scattered punctures, distance between 1–4 diameters, all punctures bearing short adpressed setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 61) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a short and adpressed seta, intervals with a row of fine punctures bearing a similar short seta, all intervals flat and shining, interval 9 with 2 setiferous pores. All femora in both sexes with teeth. All tibiae of males without modifications (Figs. 62–63). Aedeagus see Fig. 64.

Diagnosis: *Laena farkaci* n. sp. and *L. luguica* Schawaller, 2001 from Sichuan and Yunnan share the small body size, the laterally bordered subquadrate pronotum, the similar dorsal punctation and the distinctly armed femora, but *L. farkaci* n. sp. is distinguished by its shorter dorsal setation and by its completely different shape of the aedeagus. See also *L. septuagesima* n. sp. with unbordered pronotal lateral margins, and with longer and erect dorsal setation.

Laena fouquei **n. sp.**
(Figs. 93–96)

Holotype (♂): China, Yunnan, Haba Shan, 3500–4000 m, 7.–10.VI.2002, leg. S. Bečvář, R. & H. Fouquè, CSBC.

Paratypes: China, Yunnan, Haba Shan, 3150–3500 m, 6.–11.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 4 ex. CSBC, 4 ex. CRFL, 4 ex. SMNS. – China, Yunnan, Haba Shan, 3150–3500 m, 16.–18.VI.2004, leg. R. & H. Fouquè, 2 ex. CRFL, 1 ex. SMNS. – China, NW Yunnan, Haba Shan, Haba, 3200 m, 2.VII.2005, leg. M. Janata, 2 ex. BMNH. – China, NW Yunnan, Haba Shan, Haba, 4000 m, 3.VII.2005, leg. M. Janata, 1 ex. BMNH. – China, NW Yunnan, Haba Shan, Haba, 4000 m, 15.VII.2006, leg. M. Janata, 1 ex. BMNH.

Etymology: Named in honour of René Fouquè (Liberec, Czech Republic), collector of the type series.

Description: Body length 6.0–8.5 mm. Eyes (Fig. 93) not reduced, prominent. Shape of pronotum see Fig. 93, disc with large punctures, distance between 1–3 diameters, most punctures bearing short adpressed setae; surface uneven, with a pair of impressions on the disc and with an indistinct mediobasal impression, surface shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 93) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a small and adpressed seta, intervals with an irregular row of distinct punctures bearing a similar small adpressed seta, intervals 1–6 flat, interval 7 convex but not keel-like, interval 9 with 2 distinct setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 94–95). Aedeagus see Fig. 96.

Diagnosis: *Laena fouquei* n. sp., *L. chinensis* Kaszab, 1965 and *L. kubani* Schawaller, 2001, all from Yunnan and even from the same locality, share their general body size and shape, and to a certain extent their dorsal punctation and setation as well as their pronotal impressions. In *L. kubani*, however, the pronotal lateral margins are unbordered, the pronotal disc and the elytral intervals have a denser punctation, the femora are distinctly angled, and the aedeagus is different. In *L. chinensis*, the pronotum and elytral structure is similar to *L. fouquei* n. sp., but the femora bear distinct teeth, and the aedeagus is also different. See also *L. baiorum* n. sp. from Yunnan.

Laena gaoligongica **n. sp.**
(Figs. 81–84)

Holotype (♂): China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 17 ex. SMNS, 3 ex. HNHM. – China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. A. Smetana, 3 ex. CASO, 2 ex. SMNS.

Etymology: Named after the Gaoligong Shan, where the types were collected.

Description: Body length 4.5–6.0 mm. Eyes (Fig. 81) not reduced, not prominent. Shape of pronotum see Fig. 81, disc with coarse and confluent punctures, distance between 0.5–1 diameters, most punctures bearing short adpressed setae; surface uneven, with a pair of deep impressions on the disc and with an indistinct mediobasal impression, surface dull, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 81) with rows of punctures without striae, size of punctures of rows equal to pronotal punctures, each puncture bearing a small and adpressed seta, intervals with a row of distinct granules bearing a similar small adpressed seta, intervals 3 and 5 slightly, interval 7 distinctly convex but not keel-like, the other intervals flat, interval 9 with 2 distinct setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 82–83). Aedeagus see Fig. 84.

Diagnosis: This new species is characterized by the coarse confluent punctation of the pronotum, the pronotum with a pair of deep impressions and the unbordered lateral margins, the elytra with the intervals more convex than the others, unarmed femora and the shape of the aedeagus. *Laena ganzica* Schawaller, 2001 from Sichuan possesses a similar pronotum with impressions and similar elytra with elevated odd-numbered intervals, but in that species all femora bear distinct teeth and the aedeagus is shaped differently.

Laena guangxica **n. sp.**
(Figs. 9–12)

Holotype (♂): China, Guangxi, Miao'er Shan, 1800–2000 m, 15.–16.VIII.1994, leg. M. Tronquet, SMNS.

Paratypes: Same data as holotype, 1 ex. SMNS, 1 ex. CLSM.

Etymology: Named after the Province Guangxi, where the types were collected.

Description: Body length 3.5–4.3 mm. Eyes (Fig. 9) not reduced, not prominent. Shape of pronotum see Fig. 9, disc scattered with large punctures, distance between 1–3 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 9) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals slightly convex and shining, interval 9 with 4 setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 10–11). Aedeagus see Fig. 12.

Diagnosis: *Laena guangxica* n. sp., *L. daliensis* Masumoto & Yin, 1994 and *L. watanabei* Masumoto & Yin, 1993, all from Yunnan, share the general body size and shape, the subquadrate pronotum, the unarmed legs, the large dorsal punctation and the long and erect dorsal setation, but *L. guangxica* n. sp. is mainly separated by a different aedeagus and by a narrower pronotum. See also *L. guizhouica* n. sp. from Province Guizhou with a similar aedeagus but with a distinctly cordiform pronotum.

Laena guizhouica **n. sp.**
(Figs. 17–20)

Holotype (♂): China, Guizhou, Leishan County, SE Kaili, NE Leishan, eastern slope of Leigong Shan, 2.5 km E pass, 1600 m, 23.–24.VI.2001, leg. H. Schillhammer, NHMW.

Paratypes: Same data as holotype, 1 ex. NHMW, 1 ex. SMNS.

Etymology: Named after the Province Guizhou, where the types were collected.

Description: Body length 4.5–5.3 mm. Eyes (Fig. 17) not reduced, not prominent. Shape of pronotum see Fig. 17, disc scattered with large punctures, distance between 2–3 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 17) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals slightly convex and shining, interval 9 with 4 setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 18–19). Aedeagus see Fig. 20.

Diagnosis: *Laena guizhouica* n. sp., *L. daliensis* Masumoto & Yin, 1994 and *L. watanabei* Masumoto & Yin, 1993, all from Yunnan, share the general body size and shape, the unarmed legs, the large dorsal punctation and the long and erect dorsal setation; *L. guizhouica* n. sp. is mainly distinguished by a completely different, cordiform pronotum (subquadrate in the compared species). In *L. guizhouica* n. sp. the aedeagus is similar to *L. watanabei*, but differs in *L. daliensis*. See also *L. jiangxica* n. sp. and *L. moxica* n. sp.

Laena gyalthangica **n. sp.**
(Figs. 121–124)

Holotype (♂): China, N Yunnan, Zhongdian County, pass 28 km ESE Zhongdian, 3700 m, 22.VIII.2003, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 8 ex. SMNS, 1 ex. CRSW. – China, N Yunnan, Zhongdian County, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. A. Smetana, 2 ex. CASO, 2 ex. CJTK. – China, N Yunnan, Zhongdian County, 48 km N Zhongdian, 3220 m, 21.VIII.2003, leg. M. Schülke, 2 ex. SMNS. – China, N Yunnan, Zhongdian County, 48 km N Zhongdian, 3220 m, 21.VIII.2003, leg. A. Smetana, 3 ex. SMNS.

Etymology: Named after the Tibetian name Gyalthang for the village Zhongdian (Chinese name), in whose vicinity the types were collected.

Description: Body length 3.0–4.5 mm. Eyes (Fig. 121) not reduced, not prominent. Shape of pronotum see Fig. 121, disc with scattered punctures, distance between 1–2 diameters, all punctures bearing distinct adpressed setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 121) with rows of punctures without striae, punctures of rows somewhat larger than pronotal punctures, each puncture bearing a distinct adpressed seta, intervals with several fine punctures bearing a similar distinct and adpressed seta, all intervals flat and shining, interval 9 with 2 distinct setiferous pores. All

femora in both sexes without teeth. All tibiae of males without modifications (Figs. 122–123). Aedeagus see Fig. 124.

Diagnosis: *Laena gyalthangica* n. sp. belongs to a group of small species with a subquadrate flat pronotum with distinct lateral border, and without any teeth on the femora (e. g. *L. alticola* Blair, 1923, *L. daliensis* Masumoto & Yin, 1994, *L. paomaica* Schawaller, 2001 und *L. parallelocollis* Schuster, 1926), but is distinguished by the distinct dense and adpressed setation on pronotum and elytra, and by the shape of the aedeagus. Among the mentioned species only *L. daliensis* possesses also a distinct and dense dorsal setation, but in this species the bristles are long and erect, besides the different shape of the aedeagus.

Laena hlavaci **n. sp.**
(Figs. 1–4)

Holotype (♂): China, Jiangxi, Wuyi Shan Nature Reserve, Huanggan Shan, 1800–2050 m, leg. J. Cooter & P. Hlaváč, SMNS.

Paratypes: Same data as holotype, 2 ex. HNHM.

Etymology: Named in honour of Ing. Peter Hlaváč (Košice, Slovakia), one of the collectors of the type series.

Description: Body length 5.0–6.0 mm. Eyes (Fig. 1) not reduced, not prominent. Shape of pronotum see Fig. 1, disc scattered with large punctures, distance between 2–5 diameters, all punctures bearing long erect setae, surface without impressions and shagreened, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 1) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals flat and shining, interval 9 with 4 indistinct setiferous pores. All femora in both sexes with a pair of unequal teeth, in the anterior and middle femora the pair consists of a prominent and a tubercle-like tooth, in the posterior femora the pair consists of a longer and a shorter tooth. All tibiae of males without modifications (Figs. 2–3). Aedeagus see Fig. 4.

Diagnosis: See *Laena cooteri* n. sp. to distinguish the three species known from Province Jiangxi.

Laena janatai **n. sp.**
(Figs. 29–32)

Holotype (♂): China, SW Sichuan, pass Riwa to Lamuge, 4200 m, 28.VI.2006, leg. M. Janata, BMNH.

Paratype: Same data as holotype, 1 ex. SMNS.

Etymology: Named in honour of Miroslav Janata (Prague), the collector of the type series and of other *Laena* species in China.

Description: Body length 7.0 mm. Eyes (Fig. 29) not reduced, not prominent. Shape of pronotum see Fig. 29, disc with dense but not confluent punctures, distance between 0.5–2 diameters, all punctures bearing longer adpressed setae, surface with a pair of feeble impressions on the disc and shining, lateral margins finely bordered, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with sparser and finer punctation and shorter setation than on disc. Elytra (Fig. 29) with rows of punctures in feeble striae separated from the densely punctate intervals, punctures of rows slightly larger in size than pronotal punctures, most punctures bearing a short and adpressed seta, intervals with dense punctures smaller than punctures of the rows bearing a similar short adpressed seta, internal intervals flat and shining, interval 7 somewhat convex but not keel-like, interval 9 with 4 indistinct setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 30–31). Aedeagus see Fig. 32.

Diagnosis: *Laena janatai* n. sp. shares with *L. michaeli* n. sp. and *L. quinquagesima* n. sp., both from Yunnan, the extraordinary shape of the wide pronotum with a completely rounded posterior part and protruding anterior corners, but is distinguished by completely bordered lateral margins of the pronotum, unmodified male posterior tibiae, and the shape of the aedeagus. In *L. janatai* n. sp. the pronotum is widest in the middle, while it is widest in the anterior part in *L. michaeli* n. sp. and *L. quinquagesima* n. sp. See also *L. basumtsoica* n. sp.

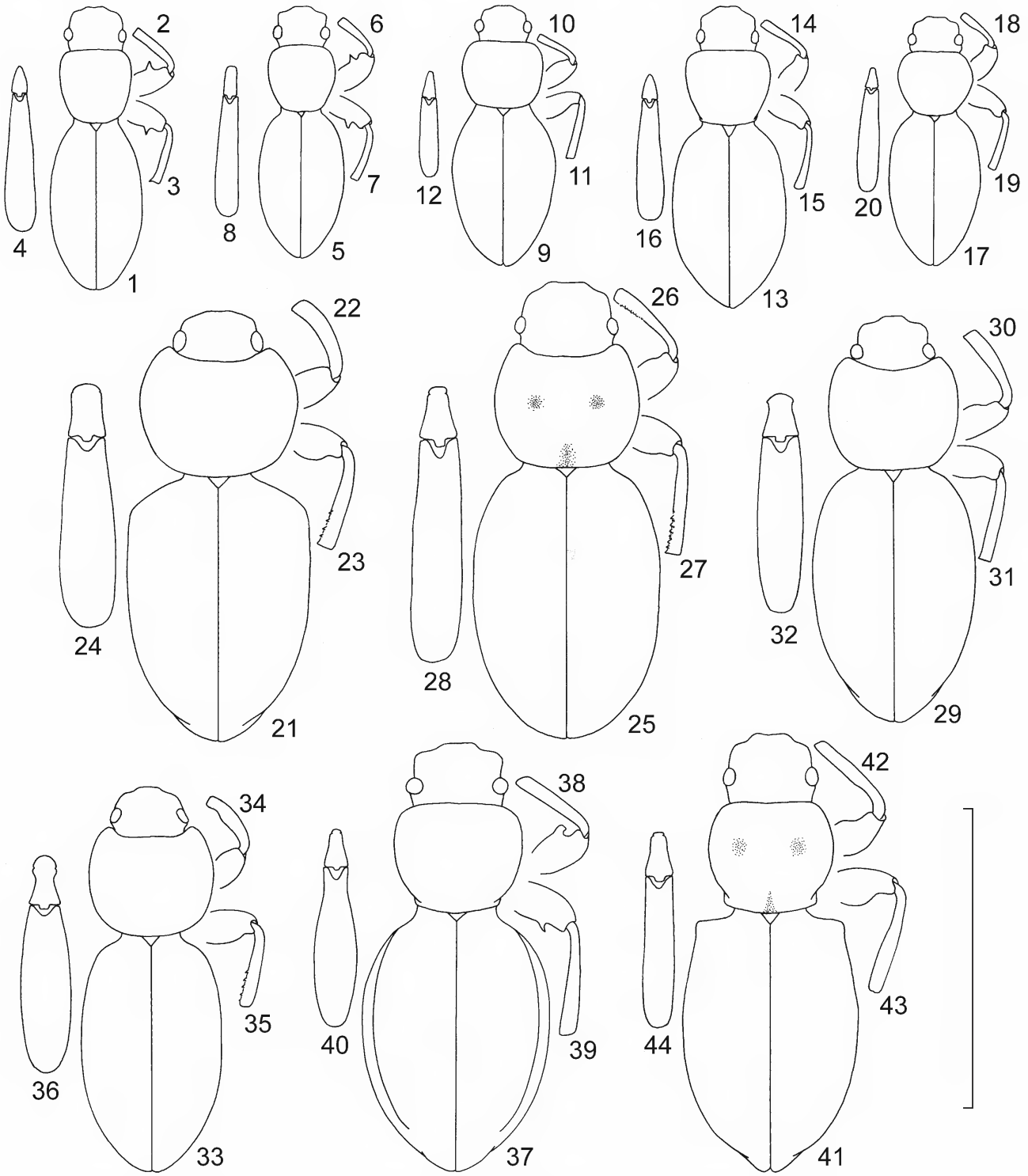
Laena jiangxica **n. sp.**
(Figs. 13–16)

Holotype (♂): China, Jiangxi, Wuyi Shan Nature Reserve, Huanggan Shan, 1800–2050 m, leg. J. Cooter & P. Hlaváč, SMNS.

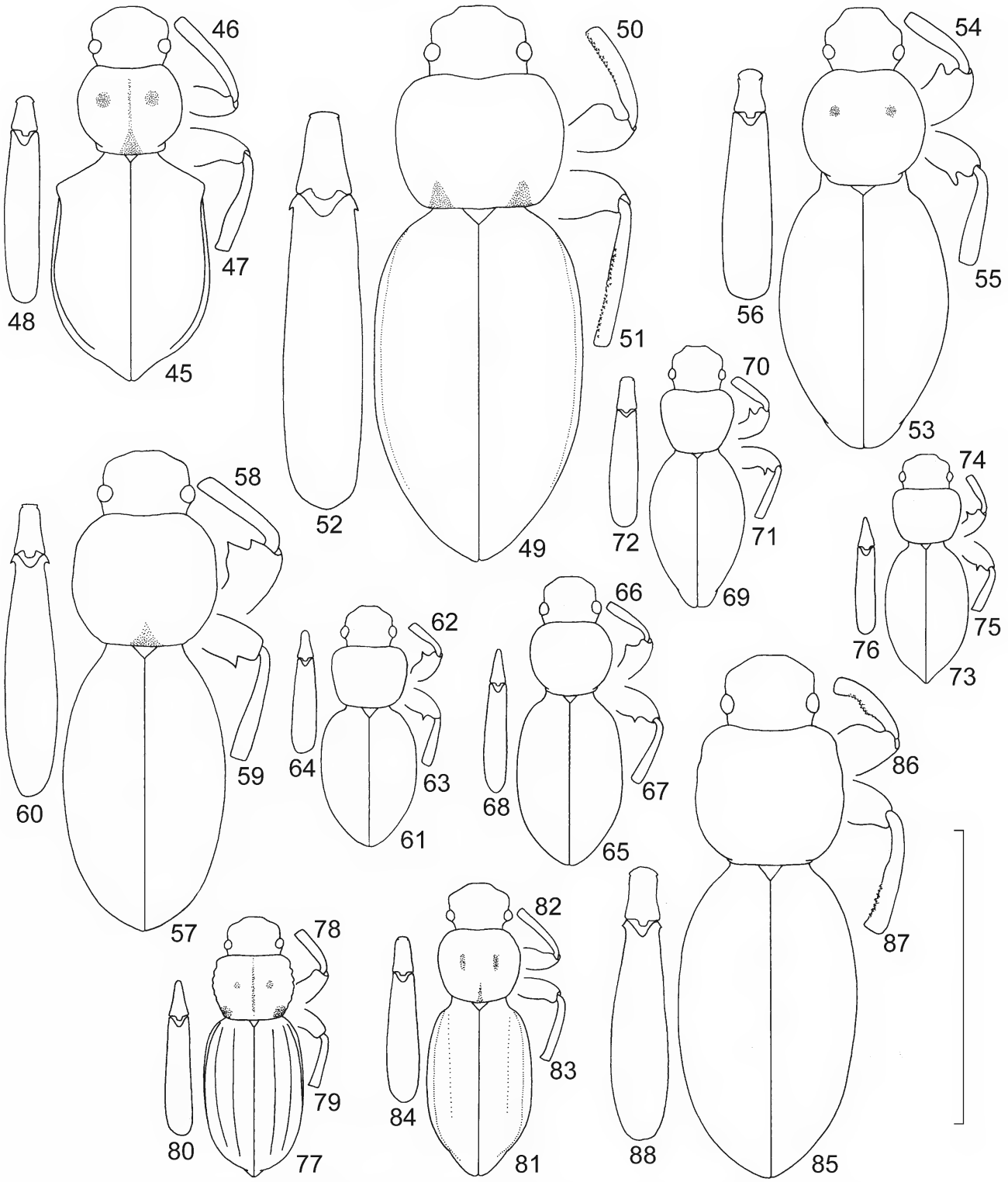
Paratypes: Same data as holotype, 2 ex. SMNS (1 ex. in bad condition without mid and hind legs).

Etymology: Named after the Province Jiangxi, were the type series was collected.

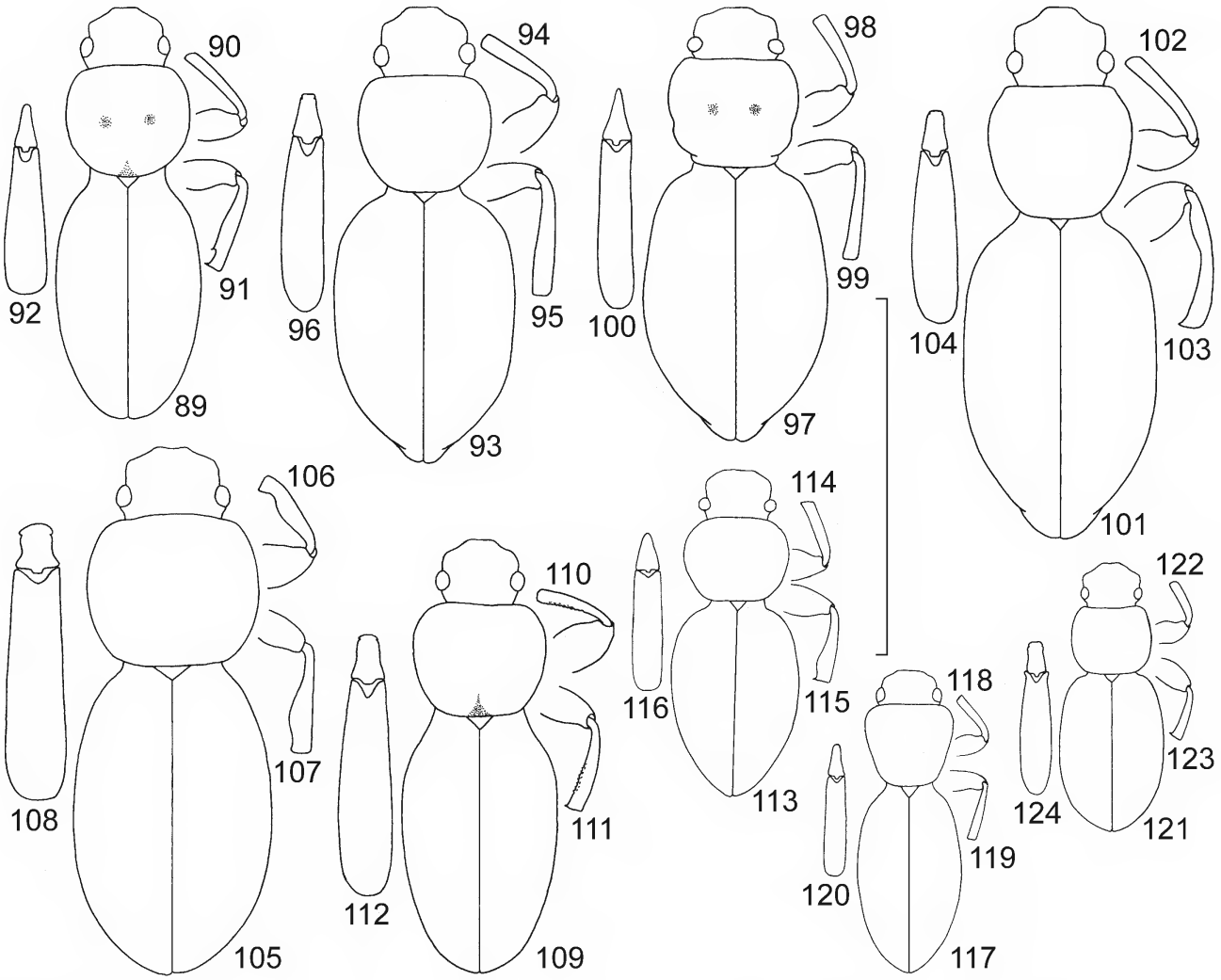
Description: Body length 5.5–6.0 mm. Eyes (Fig. 13) not reduced, not prominent. Shape of pronotum see Fig. 13, disc scattered with large punctures, distance between 2–5 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 13) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals flat and shining, interval 9 with 4 setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 14–15). Aedeagus see Fig. 16.



Figs. 1–44. Male body shape, anterior femur and tibia, posterior femur and tibia and aedeagus of *Laena* spp. – **1–4**. *L. hlavaci* n. sp. (Jiangxi), holotype. **5–8**. *L. cooteri* n. sp. (Jiangxi, Fujian), holotype. **9–12**. *L. guangxica* n. sp. (Guangxi), holotype. **13–16**. *L. jiangxica* n. sp. (Jiangxi), holotype. **17–20**. *L. guizhouica* n. sp. (Guizhou), holotype. **21–24**. *L. quinquagesima* n. sp. (Yunnan), holotype. **25–28**. *L. basumtsoica* n. sp. (Tibet), holotype. **29–32**. *L. janatai* n. sp. (Sichuan), holotype. **33–36**. *L. michaeli* n. sp. (Yunnan), holotype. **37–40**. *L. dabashanica* n. sp. (Hubei), holotype. **41–44**. *L. mirabilis* (Sichuan), non-type. – Scale line: 5.0 mm (body, legs), 2.5 mm (aedeagus).



Figs. 45–88. Male body shape, anterior femur and tibia, posterior femur and tibia and aedeagus of *Laena* spp. – **45–48**. *L. maowenica* n. sp. (Sichuan), holotype. **49–52**. *L. jinpingica* n. sp. (Sichuan), holotype. **53–56**. *L. bohrni* n. sp. (Sichuan), holotype. **57–60**. *L. sehnali* n. sp. (Sichuan), holotype. **61–64**. *L. farkaci* n. sp. (Yunnan), holotype. **65–68**. *L. lisuorum* n. sp. (Yunnan), holotype. **69–72**. *L. barkamica* n. sp. (Sichuan), holotype. **73–76**. *L. septuagesima* n. sp. (Yunnan), holotype. **77–80**. *L. davidi* n. sp. (Sichuan), holotype. **81–84**. *L. gaoligongica* n. sp. (Yunnan), holotype. **85–88**. *L. kalabi* n. sp. (Sichuan), holotype. – Scale line: 5.0 mm (body, legs), 2.5 mm (aedeagus).



Figs. 89–124. Male body shape, anterior femur and tibia, posterior femur and tibia and aedeagus of *Laena* spp. – **89–92**. *L. naxiorum* n. sp. (Yunnan), holotype. **93–96**. *L. fouquei* n. sp. (Yunnan), holotype. **97–100**. *L. alesi* n. sp. (Yunnan), holotype. **101–104**. *L. baiorum* n. sp. (Yunnan), holotype. **105–108**. *L. nujiangica* n. sp. (Yunnan), holotype. **109–112**. *L. xueshanica* n. sp. (Yunnan), holotype. **113–116**. *L. baoshanica* n. sp. (Yunnan), holotype. **117–120**. *L. moxica* n. sp. (Sichuan), holotype. **121–124**. *L. gyalthangica* n. sp. (Yunnan), holotype. – Scale line: 5.0 mm (body, legs), 2.5 mm (aedeagus).

Diagnosis: *Laena jiangxica* n. sp. is extremely similar to *L. guizhouica* n. sp. from Province Guizhou in body shape and size, the bordered lateral margins of pronotum, the dorsal punctation and setation, and the unarmed femora, but is distinguished by a slightly different pronotum (lateral sides rounder in *L. guizhouica* n. sp.), flat elytral intervals (slightly convex in *L. guizhouica* n. sp.) and a different aedeagus. See also *L. cooteri* n. sp. for separating the three species known from Province Jiangxi.

Laena jinpingica n. sp.

(Figs. 49–52)

Holotype (♂): China, Sichuan, Jinping Shan, W Mofanggou (Mo Fang Gou), 3850 m, 28.V.–4.VI.2005, leg. R. Sehnal & M. Trýzna, CJTK.

Paratypes: Same data as holotype, 13 ex. CJTK, 6 ex. SMNS.

Etymology: Named after the Jinping Shan, where the types were collected.

Description: Body length 9.5–10.5 mm. Eyes (Fig. 49) not reduced, not prominent. Shape of pronotum see Fig. 49, disc with scattered punctures, distance as 2–4 diameters, all punctures with small adpressed setae, surface flat and shagreened, with a pair of feeble impressions on the disc and 2 distinct basal impressions besides the corners, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded,

propleura with finer and sparser punctation than on disc and without setation. Elytra (Fig. 49) with rows of punctures arranged in indistinct striae, punctures of rows somewhat smaller than punctures on pronotum and extinguished in the posterior third of the elytra, most punctures with a microseta, intervals with a few scattered smaller punctures bearing each a microseta, internal intervals flat and distinctly shagreened, interval 7 distinctly convex but not keel-like, interval 9 with 4 setiferous pores. All femora in both sexes without teeth, but anterior femora with prominent angles. All tibiae of males interiorly with granules (Figs. 50–51). Aedeagus see Fig. 52.

Diagnosis: *Laena jinpingica* n. sp. is very similar to *L. turnai* Schawaller, 2001 from the same region in Sichuan (Muli). In *L. turnai*, however, the pronotum has a mediobasal impression (two lateral impressions in *L. jinpingica* n. sp.), all elytral intervals around the shoulders are slightly convex (completely flat in *L. jinpingica* n. sp. except interval 6), all femora bear teeth or at least distinct angles (only anterior femora with distinct angles in *L. jinpingica* n. sp.), the male posterior tibiae have a broadly hooked interior apex, and the aedeagus has slightly longer parameres and the basal piece without dentated apical corners.

Remarks: I hesitated for a while to distinguish the two populations as different species, but though numerous specimens of both "groups" were collected, no intermediate forms were found, therefore I now consider them as different species.

Laena kalabi **n. sp.**
(Figs. 85–88)

Holotype (♂): China, SW Sichuan, road Xiangcheng to Dérong, pass 10 km NW Xiangcheng, 3500 m, 14.VII.1994, leg. J. Kaláb, CJTK.

Paratypes: Same data as holotype, 20 ex. CJTK, 10 ex. SMNS.

Etymology: Named in honour of Jaroslav Kaláb (Kuřim, Czech Republic), collector of the type series.

Description: Body length 8.3–10.3 mm. Eyes (Fig. 85) not reduced, not prominent. Shape of pronotum see Fig. 85, disc with scattered punctures, distance as 2–5 diameters, most punctures with small adpressed setae, surface flat and shining, lateral margins bordered and somewhat irregular rounded, basal margin unbordered and not bent downwards, posterior angles rounded, propleura with similar punctation and setation as on disc. Elytra (Fig. 85) with rows of punctures without striae, punctures of rows as large as those on pronotum, most punctures bearing a microseta, intervals with a row of scattered smaller punctures bearing each a microseta, all intervals flat and shining, interval 9 with 3 indistinct setiferous pores. All femora in both sexes without teeth. Anterior and middle tibiae of males medially distinctly sinuated and with granules, posterior tibiae of males with dilatated apex and medially with granules (Figs. 86–87). Aedeagus see Fig. 88.

Diagnosis: *Laena kalabi* n. sp. shares with *L. tryznai* Schawaller, 2001 from the same region the general body shape and size, and also the shape of the aedeagus; in the latter, however, the dorsal side is dull and the pronotum is wider, and the male tibiae are only slightly modified (anterior and middle tibiae without modification, posterior tibiae with a few granules). *L. safraneki* Schawaller, 2001, also from the same region, possesses similarly modified male tibiae, but a smaller body size (5.0–7.5 mm) and an aedeagus with distinctly shorter, quadrate apicale. See also *L. nujiangica* n. sp.

Laena lisuorum **n. sp.**
(Figs. 65–68)

Holotype (♂): China, N Yunnan, Xue Shan 23 km S Zhongdian, 3675–3720 m, 2.VI.2005, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 7 ex. SMNS. – China, N Yunnan, Xue Shan 23 km S Zhongdian, 3890 m, 5.VI.2005, leg. M. Schülke, 1 ex. SMNS. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3850 m, 6.VI.2005, leg. A. Smetana, 2 ex. CASO, 1 ex. SMNS.

Etymology: Named in honour of the Chinese minority Lisu settling in northern Yunnan, where the type series was collected.

Description: Body length 4.8–6.0 mm. Eyes (Fig. 65) not reduced, not prominent. Shape of pronotum see Fig. 65, disc scattered with small punctures, distance between 2–5 diameters, all punctures bearing short adpressed setae, surface with a pair of indistinct discal impressions and slightly shagreened, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider and finer punctation and shorter setation than on disc. Elytra (Fig. 65) with rows of punctures without striae, punctures of rows distinctly larger than pronotal punctures, each puncture bearing a microseta, intervals with very few nearly indistinct punctures bearing a similar short seta; all intervals flat and shining, interval 9 with 3 setiferous pores. All femora in both sexes with distinct teeth. All tibiae of males without modifications (Figs. 66–67). Aedeagus see Fig. 68.

Diagnosis: *Laena lisuorum* n. sp. belongs to a species group with *L. fengileana* Masumoto, 1996 and *L. qinlingica* Schawaller, 2001, from Shaanxi and Sichuan, sharing the general body size and shape, the laterally unbordered pronotum and the distinct armature of the femora. However, *L. fengileana* has a narrow trapezoid pronotum with a larger punctation and a completely different aedeagus, and *L. qinlingica* (with similar shape of the pronotum and similar aedeagus) has a striking dull surface of pronotum and elytra with dense, long and erect setation.

Laena maowenica **n. sp.**
(Figs. 45–48)

Holotype (♂): China, NW Sichuan, 20 km NW Maowen, Jiuding Shan, 2150 m, 7.–28.VI.2004, leg. R. Fabbri, SMNS.

Paratypes: Same data as holotype, 1 ex. SMNS. – China, Sichuan, road from Mao Xian to Beichuan, E Mao Xian, 1900–2350 m, 27.V.–3.VI.2006, leg. A. Puchner, 1 ex. CRSW.

Etymology: Named after the city of Maowen, in whose vicinity the types were collected.

Description: Body length 7.0–7.5 mm. Eyes (Fig. 45) not reduced, not prominent. Shape of pronotum see Fig. 45, disc with dense and partly confluent punctures, distance between 0.5–1 diameters, all punctures bearing short and adpressed setae, surface uneven, with a pair of distinct impressions on the disc and with an indistinct mediobasal impression, surface dull, lateral margins somewhat marked but unbordered, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with wider punctation than and similar setation as on disc. Elytra (Fig. 45) with rows of punctures without striae, punctures of rows distinctly larger than pronotal punctures, each puncture bearing a short and adpressed seta, intervals with several fine punctures bearing a similar small seta, internal intervals flat, interval 7 distinctly keel-like, in the humeral region knob-like, external intervals without any setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 46–47). Aedeagus see Fig. 48.

Diagnosis: *Laena maowenica* n. sp. shares with *L. schuelkei* Schawaller, 2001 (also from Sichuan) the general body size and shape, the dull surface with dense punctation and dense short setation, and the keel-like elytral interval 7. In *L. maowenica* n. sp., however, the pronotum is higher convex, the elytral disc between the keel-like intervals 7 is slightly convex (absolutely flat in *L. schuelkei*), the keel-like interval 7 is knob-like anteriorly, the external elytral intervals without setiferous pores (with two prominent pores in *L. schuelkei*), and the aedeagus is different. *L. mirabilis* Kaszab, 1970 from Sichuan belongs to the same group, but the body is sligthly larger (7.8–9.0 mm), the elytral puncture rows are much finer, the elytral intervals are impunctate and without distinct setation, and the external elytral intervals besides the keel-like interval 7 are vertical in position and not visible dorsally, and the aedeagus is also different.

Laena michaeli **n. sp.**
(Figs. 33–36)

Holotype (♂): China, N Yunnan, 25 km E Zhongdian, 3300–4000 m, 12.–14.VII.1995, leg. L. Bolm, SMNS.

Paratypes: China, N Yunnan, Zhongdian County, Xue Shan, 23 km S Zhongdian, 3675–3725 m, 2.VI.2005, leg. M. Schülke, 1 ex. SMNS. – China, N Yunnan, Zhongdian County, Xue Shan near lake, 23 km S Zhongdian, 3895 m, leg. A. Smetana, 1 ex. SMNS.

Etymology: Named in honour of Michael Schülke (Berlin), who collected several species of *Laena* in China and generously deposited them in the Natural History Museum Stuttgart.

Description: Body length 6.0–6.5 mm. Eyes (Fig. 33) not reduced, not prominent. Shape of pronotum see Fig. 33, disc with dense but not confluent punctures, distance between 0.5–2 diameters, all punctures bearing short and adpressed setae, surface without impressions and dull, lateral margins bordered at least basally, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with similar punctation and setation as on disc. Elytra (Fig. 33) with rows of punctures arranged in feeble striae, not distinctly separate from the densely punctate intervals, punctures of rows slightly smaller in size than those of pronotum, each puncture with a short and adpressed seta, intervals with dense punctures of similar size to punctures of the rows bearing a similar short adpressed seta, internal intervals flat and dull, interval 7 somewhat convex but not keel-like, interval 9 with 4 setiferous pores. All femora in both sexes without teeth. Posterior tibiae of males interiorly with a few spines (Figs. 34–35). Aedeagus see Fig. 36.

Diagnosis: *Laena michaeli* n. sp. has a characteristic and extraordinary shape of the pronotum, armed posterior male tibiae and a dense dorsal punctation similar to *L. quinquagesima* n. sp. from the same region, but in that species the body is larger, the pronotum and elytra are flatter, the pronotum is completely unbordered laterally, and the aedeagus is different. See also *L. janatai* n. sp.

Laena moxica **n. sp.**
(Figs. 117–120)

Holotype (♂): China, Sichuan, Gongga Shan, Moxi, 1300 m, 11.VII.1996, leg. A. Smetana, J. Farkač & P. Kabátek, NHMB.

Paratypes: Same data as holotype, 4 ex. NHMB, 4 ex. SMNS.

Etymology: Named after the village Moxi, where the types were collected.

Description: Body length 4.5–5.0 mm. Eyes (Fig. 117) not reduced, not prominent. Shape of pronotum see Fig. 117, disc scattered with large punctures, distance between 1–3 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 117) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with very few nearly indistinct punctures bearing a similar long seta, all intervals slightly convex and shining,

interval 9 with 4 setiferous pores. All femora in both sexes without teeth. All tibiae of males without modifications (Figs. 118–119). Aedeagus see Fig. 120.

Diagnosis: *Laena moxica* n. sp. belongs to the species-group containing *L. guizhouica* n. sp., *L. daliensis* Masumoto & Yin, 1994 and *L. watanabei* Masumoto & Yin, 1993 because of the the general body size and shape, the unarmed legs, the large dorsal punctation and the long and erect dorsal setation, but can be recognized by the long trapezoid pronotum (subquadrate in *L. daliensis* and *L. watanabei*, cordiform in *L. guizhouica* n. sp.) and by the shape of the aedeagus.

Laena naxiorum **n. sp.**
(Figs. 89–92)

Holotype (♂): China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 5.–15.VI.2005, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 4 ex. SMNS. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 5.–15.VI.2005, leg. A. Smetana, 3 ex. SMNS. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 6.–15. VI.2005, leg. D. Wrase, 1 ex. CJTK. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3850 m, 6.VI.2005, leg. A. Smetana, 2 ex. CASO. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 6.VI.2005, leg. M. Schülke, 7 ex. SMNS. – China, N Yunnan, 23 km S Zhongdian, Xue Shan, 3675–3725 m, 2.VI.2005, leg. M. Schülke, 1 ex. SMNS. – China, N Yunnan, Xue Shan, 10 km SW Zhongdian, 3800 m, 20.VIII.2003, leg. A. Smetana, 5 ex. SMNS. – China, N Yunnan, Xue Shan, 10 km SW Zhongdian, 3800 m, 20.VIII.2003, leg. D. Wrase, 1 ex. CJTK. – China, N Yunnan, Xue Shan near Zhongdian, 3900–4200 m, 23.–25.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 7 ex. NHMB. – China, N Yunnan, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. M. Schülke, 2 ex. CJTK, 1 ex. SMNS. – China, N Yunnan, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. A. Smetana, 1 ex. CASO.

Etymology: Named in honour of the Chinese minority Naxi settling in northern Yunnan, where the type series was collected.

Description: Body length 5.5–7.2 mm. Eyes (Fig. 89) not reduced, not prominent. Shape of pronotum see Fig. 89, disc with scattered punctures of somewhat different size, distance between 2–4 diameters, all punctures bearing short adpressed setae, surface with a pair of indistinct discal impressions and a feeble mediobasal impression and slightly shagreened, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 89) with rows of punctures without striae, punctures of rows smaller than pronotal punctures, each puncture bearing a short and adpressed seta, intervals with very few nearly indistinct punctures bearing a similar short seta, all intervals flat and shining, interval 9 with 4 indistinct setiferous pores. All femora in both sexes without teeth. Posterior tibiae of males with a distinct spine in the distal third (Figs. 90–91). Aedeagus see Fig. 92.

Diagnosis: See *Laena xueshanica* n. sp. from the same locality. See also *L. alesi* n. sp.

Laena nujiangica **n. sp.**
(Figs. 105–108)

Holotype (♂): China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 7 ex. SMNS, 2 ex. CJTK. – China, N Yunnan, Nujiang Lisu Autonomous Prefecture, Gongshan County, Gaoligong Shan, 3000–3050 m, 21.VI.2005, leg. A. Smetana, 3 ex. CASO.

Etymology: Named after the Nujiang (= Salween) Lisu Autonomous Prefecture, where the type series was collected.

Description: Body length 6.0–7.8 mm. Eyes (Fig. 105) not reduced, not prominent. Shape of pronotum see Fig. 105, disc with scattered punctures, distance as 3–6 diameters, most punctures with longer erect setae, surface flat and shining, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded, propleura nearly impunctate and without setation. Elytra (Fig. 105) with rows of punctures without striae, these rows partly extinguished in posterior part, punctures of rows larger than punctures on pronotum, punctures without setae, intervals with very few scattered smaller punctures bearing each a small erect seta, all intervals flat and shining, interval 9 with 3 indistinct setiferous pores. All femora in both sexes without teeth. Anterior tibiae of males with distinct mediobasal excavation, middle and posterior tibiae of males with dilatated apex, all male tibiae medially with long and dense setation (Figs. 106–107). Aedeagus see Fig. 108.

Diagnosis: *Laena nujiangica* n. sp. can be recognized by the modified male anterior tibiae with a distinct mediobasal excavation, by a subquadrate shining pronotum with fine punctation without impressions and bordered lateral margins, by nearly impunctate elytral intervals, and by the shape of the aedeagus with short quadrate apicale. *L. safraneki* Schawaller, 2001 from adjacent southeastern Tibet has similarly modified male anterior tibiae and a similar shape of the aedeagus, but in that species the dorsal surface is dull shagreened and the posterior male tibiae are differently modified with interior granules. *L. kalabi* n. sp. from Sichuan and *L. tuntalica* Schawaller, 2001 from Sichuan and Tibet have also similarly modified anterior male tibiae, but possess, besides other characters, different shapes of the aedeagus with distinctly longer apicale.

Laena quinquagesima **n. sp.**
(Figs. 21–24)

Holotype (♂): China, N Yunnan, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. M. Schülke, SMNS.

Paratypes: China, N Yunnan, pass 28 km ESE Zhongdian, 3700–3750 m, 22.VIII.2003, leg. D. Wrase, 2 ex. CJTK. –

China, N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. M. Schülke, 2 ex. SMNS. – China, N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.–24.VIII.2003, leg. D. Wrase, 3 ex. CJTK. – China, N Yunnan, 29 km ESE Zhongdian, Bitai Hai Lake area, 3540 m, 1.VI.2005, leg. D. Wrase, 1 ex. CJTK. – China, N Yunnan, 35 km ESE Zhongdian, 3450 m, 3.VI.2005, leg. M. Schülke, 1 ex. SMNS. – China, N Yunnan, 35 km ESE Zhongdian, 3450 m, 3.VI.2005, leg. D. Wrase, 3 ex. CJTK, 2 ex. SMNS. – China, N Yunnan, Xue Shan near Zhongdian, 3800 m, 26.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 4 ex. NHMB. – China, N Yunnan, 17 km NW Zhongdian, 3500–4000 m, 15.–23.V.1999, leg. L. & R. Businský, 4 ex. CSBC, 1 ex. SMNS. – China, NW Yunnan, Zhongdian, Haxube Shan, W slope between Tuguancun and Xiaozhongdian, 3700–3900 m, 29.IV.1998, leg. M. Janata, 2 ex. CKBB. – NW Yunnan, Haba Shan, Haba, 3200 m, 2.VII.2005, leg. M. Janata, 1 ex. BMNH.

Etymology: Named after the Latin "quinquagesimus", because this is the 50th new species of *Laena* from China treated by the author during the preparation of this manuscript.

Description: Body length 7.5–9.5 mm. Eyes (Fig. 21) not reduced, not prominent. Shape of pronotum see Fig. 21, disc with dense and partly confluent punctures, distance between 0.5–1 diameters, all punctures bearing short and adpressed setae, surface somewhat uneven and dull, lateral margins unbordered, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with similar punctation and setation as on disc. Elytra (Fig. 21) with rows of punctures without striae not distinctly separated from the densely punctate intervals, punctures of rows equal in size to pronotal punctures, each puncture bearing a short and adpressed seta, intervals with dense punctures of similar size as punctures of the rows bearing a similar short adpressed seta, internal intervals flat and dull, interval 7 distinctly convex but not keel-like, interval 9 with 4 setiferous pores. All femora in both sexes without teeth. Posterior tibiae of males interiorly with a few spines (Figs. 22–23). Aedeagus see Fig. 24.

Diagnosis: The species is characterized by the shape of its wide pronotum with a completely rounded posterior part, protruding anterior corners and unbordered lateral margins, its dense confluent dorsal punctation, and also by its elytral intervals with short and adpressed setae, its convex but not keeled elytral interval 7, unarmed femora and armed posterior male tibiae, and the shape of its aedeagus. *Laena quinquagesima* n. sp. belongs to the group of species with a flat elytral disc and keel-like elytral intervals, including *L. mirabilis* Kaszab, 1970 and *L. mulica* Schawaller, 2001, both from Sichuan, but can be immediately separated by the characteristic shape of the pronotum. *L. michaeli* n. sp. from the same region possesses a similar shape of the pronotum, similarly armed posterior male tibiae and a dense dorsal punctation, but in that species the body is smaller, pronotum and elytra are more convex, the pronotum is bordered laterally, at least in its basal part, and the aedeagus is different. See also *L. janatai* n. sp.

Laena sehnali **n. sp.**

(Figs. 57–60)

Holotype (♂): China, SW Sichuan, NNE Eryizuxiang, SW slopes, V.2004, leg. M. Häckel & R. Sehnal, CJTK.

Paratypes: Same data as holotype, 4 ex. CJTK, 3 ex. SMNS. – China, Sichuan, San Ya (Eryizuxiang), 3800 m, 10.VI.2005, leg. R. Sehnal & M. Trýzna, 1 ex. CJTK. – China, Sichuan, Daxue Shan, N San Ya, 3040 m, 6.–12.VI.2005, leg. R. Sehnal & M. Trýzna, 1 ex. CJTK. – China, W Sichuan, Jiulong County, N Yalong Jiang great riverbend, 2300–3800 m, 12.–16.VII.2001, leg. L. & R. Businský, 1 ex. SMNS.

Etymology: Named in honour of Rostislav Sehnal (Unhost, Czech Republic), one of the collectors of the type series.

Description: Body length 7.0–9.5 mm. Dorsal side with feeble metallic shine. Eyes (Fig. 57) not reduced, not prominent. Shape of pronotum see Fig. 57, disc with scattered punctures, distance as 2–5 diameters, some punctures with longer adpressed setae, surface flat and shining, with a pair of feeble impressions on the disc and a distinct mediobasal impression, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded, propleura with much finer and sparser punctation than on disc and without setation. Elytra (Fig. 57) with rows of punctures without striae, punctures of rows as large as punctures on pronotum, punctures without setae, intervals with a few scattered smaller punctures, also without setae, all intervals flat and shining, interval 9 posteriorly with 3 setiferous pores. All femora in both sexes with distinct teeth, anterior femur in males extraordinarily thick and with an additional tooth-like anterior corner. Anterior and middle tibiae of males without modifications, posterior tibiae of males slightly S-shaped (Figs. 58–59). Aedeagus see Fig. 60.

Diagnosis: *Laena sehnali* n. sp. is characterized by its large body size, its weak dorsal metallic shine, its broad disc-like pronotum with bordered lateral margins, its distinct armature of the femora, particularly of the male anterior femora, and the shape of the aedeagus; the species cannot be confused with any other Chinese species.

Laena septuagesima **n. sp.**

(Figs. 73–76)

Holotype (♂): China, N Yunnan, pass 28 km ESE Zhongdian, 3700 m, 22.VIII.2003, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 2 ex. SMNS. – China, N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. M. Schülke, 8 ex. SMNS. – China, N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.–24.VIII.2003, leg. D. Wrase, 6 ex. CJTK. – China, N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. A. Smetana, 8 ex. SMNS, 2 ex. CASO, 2 ex. CJTK. – China, N Yunnan, 33 km ESE Zhongdian, 3200 m, 24.VIII.2003, leg. A. Smetana, 1 ex. SMNS.

Etymology: Named after the Latin "septuagesimus", because this is the 70th new species of *Laena* from China treated by the author during the preparation of this manuscript.

Description: Body length 3.0–4.2 mm. Eyes (Fig. 73) not reduced, not prominent. Shape of pronotum see Fig. 73, disc with scattered punctures, distance between 1–4 diameters, all punctures bearing long erect setae, surface without impressions and shining, lateral margins marked but unbordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 73) with rows of punctures without striae, punctures of rows equal in size to pronotal punctures, each puncture bearing a long and erect seta, intervals with a row of fine punctures bearing a similar long seta, all intervals flat and shining, interval 9 with 2 setiferous pores. All femora in both sexes with teeth. All tibiae of males without modifications (Figs. 74–75). Aedeagus see Fig. 76.

Diagnosis: *Laena septuagesima* n. sp. belongs to the group of small species with subquadrate pronotum and distinctly armed femora around *L. daxueica* Schawaller, 2001 from Sichuan and *L. farkaci* n. sp. from Yunnan. With *L. septuagesima* n. sp. *L. daxueica* shares the unbordered pronotal lateral margins, but *L. daxueica* has a shorter adpressed dorsal setation and a different aedeagus. *L. farkaci* n. sp. has bordered pronotal lateral margins, and also a shorter adpressed dorsal setation and a different aedeagus.

Laena xueshanica **n. sp.**
(Figs. 109–112)

Holotype (♂): China, N Yunnan, Xue Shan, near lake 23 km S Zhongdian, 3895 m, 5.–15.VI.2005, leg. M. Schülke, SMNS.

Paratypes: Same data as holotype, 10 ex. SMNS. – China, N Yunnan, Xue Shan, near lake 23 km S Zhongdian, 3895 m, 5.VI.2005, leg. A. Smetana, 13 ex. SMNS, 4 ex. CRFL. – China, N Yunnan, Xue Shan, near lake 23 km S Zhongdian, 3895 m, 15.VI.2005, leg. A. Smetana, 5 ex. CASO. – China, N Yunnan, Xue Shan, near lake 23 km S Zhongdian, 3850 m, 6.VI.2005, leg. A. Smetana, 6 ex. HNHM. – China, N Yunnan, Xue Shan, 23 km S Zhongdian, 3675–3725 m, 2.VI.2005, leg. D. Wrase, 1 ex. CJTK. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 6.VI.2005, leg. M. Schülke, 11 ex. SMNS. – China, N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895 m, 5.–15.VI.2005, leg. D. Wrase, 8 ex. CJTK. – China, N Yunnan, Xue Shan, 10 km SW Zhongdian, 3800 m, 20.VIII.2003, leg. A. Smetana, 14 ex. SMNS, 4 ex. NHMW, 4 ex. OUMNH, 1 ex. CASO. – China, N Yunnan, Xue Shan, 10 km SW Zhongdian, 3700–3800 m, 20.VIII.2003, leg. D. Wrase, 7 ex. CJTK. – China, N Yunnan, Mts. 15 km W Zhongdian, 3800–4200 m, 22.–24.VI.1994, leg. J. Farkač & D. Král, 2 ex. NHMB. – China, N Yunnan, Xue Shan near Zhongdian, 3800 m, 23.–26.VI.1996, leg. J. Farkač, P. Kabátek & A. Smetana, 1 ex. NHMB. – China, N Yunnan, Xue Shan near Zhongdian, 4000–4100 m, 23.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 8 ex. NHMB. – China, N Yunnan, Xue Shan near Zhongdian, 4050 m, 24.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 46 ex. NHMB, 3 ex. CJTK. – China, N Yunnan, Xue Shan near Zhongdian, 3900 m, 25.VI.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 23 ex. NHMB.

Etymology: Named after the Xue Shan, where the types were collected.

Description: Body length 4.5–6.5 mm. Eyes (Fig. 109) not reduced, not prominent. Shape of pronotum see Fig. 109, disc with scattered punctures of somewhat different size, distance between 1–4 diameters, all punctures bearing short adpressed setae, surface with a slight mediobasal impression and weakly shagreened, lateral margins bordered, basal margin unbordered and not bent downwards, posterior angles rounded and indistinct, propleura with wider punctation and shorter setation than on disc. Elytra (Fig. 109) with rows of punctures without striae, punctures of rows smaller than pronotal punctures, each puncture bearing a short and adpressed seta, intervals with very few nearly indistinct punctures bearing a similar short seta, all intervals flat and shining, interval 9 with 4 indistinct setiferous pores. All femora in both sexes without teeth. All tibiae of males with a few indistinct granules at the inner side (Figs. 110–111). Aedeagus see Fig. 112.

Diagnosis: *Laena xueshanica* n. sp., *L. naxiorum* n. sp. from the same locality and *L. cholanica* Schawaller, 2001 from adjacent southeastern Tibet are extremely similar and share the medium-sized body, the flat subquadrate and laterally bordered pronotum, the adpressed shorter setation and the unarmed femora. All three can be separated by distinctly different aedeagi (apicale broad spadelike in *L. xueshanica* n. sp., long triangular in *L. naxiorum* n. sp., short triangular in *L. cholanica*) and by unmodified posterior tibiae in *L. cholanica* or differently modified posterior tibiae in *L. naxiorum* n. sp. with a single spine or with a few distinct granules in *L. xueshanica* n. sp. The elytra are long parallel in *L. cholanica* and of oval shape in *L. naxiorum* n. sp. and *L. xueshanica* n. sp. See also under *L. alesi* n. sp.

5 New records of previously known species of *Laena*

Laena alticola Blair, 1923

New material: Tibet, N Mt. Everest, Rongbuk Valley (type locality), 5200 m, 9.–11.VII.1993, leg. T. Solhby, 5 ex. SMNS. – S Tibet, Monda La, 20 km from Lhodak, 5200 m, 16.VI.2001, leg. A. Wrzecionko, 1 ex. CJTK, 1 ex. SMNS. – S Tibet, Karo La, 30 km E Nakatse, 5120 m, 1.VI.2005, leg. A. Wrzecionko, 7 ex. CJTK, 2 ex. SMNS.

Laena angulifemoralis Masumoto, 1996

New material: Yunnan, Jizu Shan, 2500–2700 m, 6.–10.VII.1994, leg. V. Kubáň, 1 ex. CJTK, 1 ex. SMNS.

Laena baishuica Schawaller, 2001

New material: N Yunnan, 30 km N Lijiang, E Yulongxue Shan, 2800–2900 m, 13.VIII.2003, leg. A. Smetana, 2 ex. SMNS.

Laena becvari Schawaller, 2001

New material: Yunnan, Haba Shan, 3150–3500 m, 6.–11.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 9 ex. CRFL, 3 ex. SMNS. – N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. A. Smetana, 1 ex. SMNS, 1 ex. CASO. – N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. M. Schülke, 2 ex. SMNS. – N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.–24.VIII.2003, leg. D. Wrase, 1 ex. CJTK. – NW Yunnan, Haba Shan, Haba, 3200 m, 15.VII.2006, leg. M. Janata, 1 ex. BMNH.

Laena bifoveolata Reitter, 1889

New material: W Henan, Funju Shan, Shiren Shan, 1400–1900 m, 9.VII.2006, leg. J. Turna, 1 ex. CJTK. – Shaanxi, Daba Shan, 20 km SEE Zhenping, 1700 m, 26.VI.2002, leg. Stary, 1 ♀ CRSW. – Shaanxi, Qinling Shan, Zhouzhi to Foping, 2000 m, 1.VII.2002, leg. Stary, 1 ♀ SMNS. – S Shaanxi, Li Shan, SE slopes of Shun Wang Ping, 2040–2200 m, 13.V.–4.VII.2006, leg. J. Turna, 1 ex. CJTK. – Hubei, Daba Shan, 13 km NW Muyuping, 1900 m, 16.VII.2002, leg. Stary, 1 ex. CRSW, 1 ex. SMNS. – W Hubei, Dashennongjia Mts., 2700 m, 20.V.–7.VI.2005, leg. J. Turna, 2 ex. CJTK. – Sichuan, Gongga Shan near Moxi, around camp 3, 3000–3300 m, 25.–27.VII.1994, leg. W. Heinz, 1 ex. SMNS. – Sichuan, Gongga Shan, Hailuogou, above camp 3, 3100 m, 8.VII.1996, leg. A. Smetana, J. Farkač & P. Kabátek, 1 ex. NHMB. – Sichuan, Gongga Shan, Hailuogou, 2900–3200 m, leg. J. Farkač & D. Král, 1 ex. NHMB.

Laena brendelli Schawaller, 2001

New material: N Yunnan, 33 km ESE Zhongdian, 3200 m, 24.VIII.2003, leg. M. Schülke, 2 ex. SMNS. – N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.VIII.2003, leg. M. Schülke, 5 ex. SMNS. – N Yunnan, 36 km ESE Zhongdian, 3500–3550 m, 23.–24.VIII.2003, leg. D. Wrase, 4 ex. CJTK. – Yunnan, Haba Shan, 3150–3500 m, 6.–11.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 3 ex. CRFL, 2 ex. SMNS.

Laena businskyorum Schawaller, 2001

New material: NW Yunnan, 25–35 km SE Deqen, 3100–3900 m, 20.–22.VII.1996, leg. L. & R. Businský, 3 ex. CJTK.

Laena chinensis Kaszab, 1965

New material: N Yunnan, Diancang Shan 5 km SSW Dali, 2800 m, 26.VIII.2003, leg. A. Smetana, 2 ex. CASO. – Yunnan, Jizu Shan, 2500–2700 m, 6.–10.VII.1994, leg. V. Kubáň, 2 ex. CJTK. – N Yunnan, Diancang Shan W Dali, 2650–2800 m, 26.VIII.–1.IX.2003, leg. D. Wrase, 2 ex. CJTK.

Laena Cholanica Schawaller, 2001

New material: SE Tibet, pass 50 km S Markam, 4400 m, 24.–27.VI.1997, leg. J. Turna, 5 ex. CJTK.

Laena daliensis Masumoto & Yin, 1994

New material: N Yunnan, Diancang Shan W Dali, 2650–3000 m, 28.VIII.–1.IX.2003, leg. M. Schülke, 25 ex. SMNS. – N Yunnan, Diancang Shan W Dali, 2650–2750 m, 17.VI.2005, leg. M. Schülke, 6 ex. SMNS. – N Yunnan, Diancang Shan 5 km SSW Dali, 2650–3000 m, 29.–31.VIII.2003, leg. A. Smetana, 10 ex. SMNS, 12 ex. CASO. – Yunnan, SE Dali, Weibao Shan, W slope, 2000–2800 m, 23.VI.2004, leg. R. & H. Fouquè, 1 ex. CRFL.

Laena daxueica Schawaller, 2001

New material: W Sichuan, Ya'an Prefecture, Shimian County, Xiaoxiang Ling, Caluo, 11 km S Shimian, 1250 m, 7.VII.1999, leg. A. Pütz, 1 ex. CAPE. – W Sichuan, Ya'an Prefecture, Shimian County, Xiaoxiang Ling, 7 km S Liziping, 35 km S Shimian, 1600 m, 7.VII.1999, leg. A. Pütz, 1 ex. CAPE, 1 ex. SMNS.

Laena diancangica Schawaller, 2001

New material: N Yunnan, Diancang Shan W Dali, 2650–2750 m, 17.VI.2005, leg. M. Schülke, 1 ex. SMNS.

Laena dickorei Schawaller, 2001

New material: E Tibet, 90 km W Gyamda, Basum Tso (Tsongo), 4310 m, 7.VI.2005, leg. A. Wrzecionko, 1 ex. CJTK. – E Tibet, 90 km W Gyamda, Basum Tso, 3700 m, 17.VI.2001, leg. A. Wrzecionko, 1 ex. CJTK.

Laena emeishana Masumoto, 1996

New material: W Sichuan, W Zhier (= Zi'er), 4240 m, 5.VI.2006, leg. R. Sehnal & M. Trýzna, 2 ex. BMNH.

Laena fengileana Masumoto, 1996

New material: Shaanxi, Qinling Shan, Zhouzhi to Foping, 2000 m, 1.VII.2002, leg. Stary, 8 ex. CRSW, 2 ex. SMNS. – S Shaanxi, Qinling Shan, pass on road Zhouzhi to Foping, 105 km SW Xi'an, 1990 m, 2.–4.VII.2001, leg. D. Wrase, 6 ex. DEI, 4 ex. SMNS, 3 ex. CJTK. – Shaanxi, Qinling Shan, pass on road Zhouzhi to Foping, 105 km SW Xi'an, 1990 m, 2.–4.VII.2001, leg. A. Smetana, 6 ex. SMNS, 2 ex. CASO. – S Shaanxi, 45 km SSW Xi'an, Qinling Shan, W pass on road Xi'an to Shagoujie, 2600 m, 25.VII.2001, leg. A. Smetana, 4 ex. SMNS. – S Gansu, Min Shan, 60 km NW Wudu, 2000 m, 10.–20.VI.2005, leg. V. Patrikeev, 2 ex. BMNH.

Laena ganzica Schawaller, 2001

New material: W Sichuan, Ya'an Prefecture, Tianquan County, W Erlang Shan pass, 2900 m, 20.–22.VI.1999, leg. A. Pütz, 3 ex. CAPE, 1 ex. SMNS.

Laena gyamdaica Schawaller, 2001

New material: E Tibet, 90 km W Gyamda, Basum Tso, 3700 m, 17.VI.2001, leg. A. Wrzecionko, 2 ex. CJTK, 2 ex. SMNS. – E Tibet, 90 km W Gyamda, Basum Tso (Tsongo), 4312 m, 7.VI.2005, leg. A. Wrzecionko, 2 ex. CJTK.

Laena habashanica Schawaller, 2001

New material: Yunnan, Haba Shan, 3150–3500 m, 16.–18.VI.2004, leg. R. & H. Fouquè, 20 ex. CRFL. – Yunnan, Haba Shan, 3150–3500 m, 6.–11.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 90 ex. CRFL, 6 ex. SMNS, 4 ex. HNHM. – Yunnan, Haba Shan, Haba, 3200 m, 2.–3.VII.2005, leg. M. Janata, 9 ex. BMNH. – Yunnan, Haba Shan, Haba, 3200 m, 15.VII.2006, leg. M. Janata, 3 ex. BMNH.

Laena haigouica Schawaller, 2001

New material: S Gansu, Min Shan, Baima pass, 3500 m, 6.VII.2004, leg. V. Patrikeev, 1 ex. cmLS. – S Gansu, Min Shan, 60 km NW Wudu, 2000 m, 10.–20.VI.2005, leg. V. Patrikeev, 3 ex. BMNH. – N Sichuan, Min Shan, Baima pass, 3500 m, 12.VII.2004, leg. V. Patrikeev, 1 ex. BMNH. – N Sichuan, Min Shan, Juijaigow, 2000 m, 10.–20.VII.2004, leg. V. Patrikeev, 1 ex. BMNH.

Laena heinzi Schawaller, 2001

New material: S Tibet, 90 km E Lhasa, 3800 m, 4.–5.VI.1996, leg. A. Wrzecionko, 3 ex. SMNS.

Remarks: The new material possesses a long setation on both pronotum and elytra in contrary to the types which have a long setation on the pronotum and only a very short setation on the elytra (setae here broken?). All other characters coincide, also the confused elytral punctation not arranged in rows.

Laena hengduanica Schawaller, 2001

New material: Sichuan, pass N Zhendu, 3700–3800 m, 25.VI.1996, leg. D. Erber, 2 ex. SMNS. – N Yunnan, Baima Shan, pass 12 km SE Deqen, 4085 m, 10.VI.2005, leg. M. Schülke, 4 ex. SMNS. – N Yunnan, Baima Shan, pass 12 km SE Deqen, 4085 m, 10.VI.2005, leg. A. Smetana, 2 ex. SMNS. – N Yunnan, Baima Shan, pass 25 km SE Deqen, 4225 m, 8.VI.2005, leg. A. Smetana, 1 ex. SMNS, 2 ex. CASO. – NW Yunnan, 25–35 km SE Deqen, 3100–3900 m, 20.–22.VII.1996, leg. L. & R. Businský, 2 ex. CJTK. – N Yunnan, Baima Shan, pass 12 km SE Deqen, 4300 m, 10.VI.2005, leg. D. Wrase, 4 ex. CJTK.

Laena houzhenzica Schawaller, 2001

New material: S Shaanxi, Daba Shan, pass 22 km NW Zhenping, 2850 m, 13.VII.2001, leg. D. Wrase, 1 ♀ SMNS. – Shaanxi, Daba Shan, pass 22 km NW Zhenping, 2850 m, 14.VII.2001, leg. A. Smetana, 4 ♀♀ SMNS, 2 ♀♀ CASO.

Laena hubeica Schawaller, 2001

New material: Hubei, Daba Shan, 13 km NW Muyuping, 1900 m, 16.VII.2002, leg. Stary, 1 ex. CRSW, 1 ex. SMNS. – W Hubei, Daba Shan pass E Mt. Dashennongjia, 12 km NW Muyuping, 1950 m, 16.–22.VII.2001, leg. A. Smetana, 6 ex. SMNS, 2 ex. CASO. – W Hubei, Mt. Dashennongjia, 2100–2900 m, 10.–14.VI.2002, leg. J. Turna, 2 ex. CJTK. – W Hubei, Mt. Dashennongjia, 2700 m, 20.V.–7.VI.2005, leg. J. Turna, 2 ex. CJTK.

Laena kangdingica Schawaller, 2001

New material: W Sichuan, 20 km NNW Sabdé, 2000–3500 m, 18.–20.VI.1994, leg. J. Kaláb, 1 ex. CJTK. – SW Sichuan, Sabdé, 3400 m, 25.VI.2001, leg. M. Janata, 1 ex. BMNH. – W Sichuan, Sa'de (= Sabdé), 3500–3800 m, V.2004, leg. M. Häckel & R. Sehnal, 4 ex. CJTK. – Sichuan, Ganzi Tibetian Autonomous Prefecture, 6 km WSW Yajiang, Shaluli Shan, 3250 m, 4.VII.1999, leg. A. Pütz, 1 ex. CAPE.

Laena kubani Schawaller, 2001

New material: Yunnan, Haba Shan, 3150–3500 m, 6.–11.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 15 ex. CRFL, 5 ex. SMNS. – Yunnan, Haba Shan, 3500–4000 m, 12.–16.VI.2004, leg. R. & H. Fouquè, 4 ex. CRFL. – N Yunnan, 33 km ESE Zhongdian, 3200 m, 24.VIII.2003, leg. A. Smetana, 1 ex. CASO.

Laena langmusica Schawaller, 2001

New material: Gansu, Min Shan, Baima pass, 3500 m, 6.VII.2004, leg. V. Patrikeev, 1 ex. cmLS. – N Sichuan, Min Shan, Baima pass, 3500 m, 12.VII.2004, leg. V. Patrikeev, 2 ex. BMNH. – N Sichuan, Min Shan, Jujiaigow, 2000 m, 10.–20.VII.2004, leg. V. Patrikeev, 1 ex. SMNS. – N Sichuan, Jiuding Shan, 3300–3500 m, 31.VII.–1.VIII.1994, leg. M. Tronquet, 1 ex. SMNS, 2 ex. CLSM. – N Sichuan, Songpan, Zhaga Waterfall, 3050 m, 5.VIII.1994, leg. M. Tronquet, 1 ex. SMNS.

Laena luguica Schawaller, 2001

New material: Sichuan, Jinping Shan, W Mofanggou (Mo Fang Gou), 3350 m, 28.V.–4.VI.2005, leg. R. Sehnal & M. Trýzna, 3 ex. CJTK, 1 ex. SMNS.

Remarks: These four specimens are somewhat larger (6.3–7.5 mm) than the five type specimens (4.8–6.0 mm), all other characters coincide, also the shape of the aedeagus. Additionally, the newly collected specimens originate from the same border region in Sichuan and Yunnan, where the types were collected.

Laena mirabilis Kaszab, 1970
(Figs. 41–44)

New material: W Sichuan, Jiajin Shan, 18 km E Jintang, 3550–3650 m, 11.–24.VI.2004, leg. R. Fabbri, 5 ex. SMNS. – Central Sichuan, Jiajin Shan, Jintang, 3400 m, 15.VI.2002, leg. M. Janata, 4 ex. CHHR, 1 ex. SMNS. – NW Sichuan, between Sanggarmai and Sanggarpar, 3500 m, 8.–29.VI.2004, leg. R. Fabbri, 3 ex. SMNS. – W Sichuan, Qionglai Shan, Mou Pi Shan, Barkam, 15 km S Zhuokeji, 3100–3750 m, 10.–30.VI.2004, leg. R. Fabbri, 3 ex. SMNS. – W Sichuan, S Barkam, between Lianghekou and Fubian, 3450–3650 m, 10.–30.VI.2004, leg. R. Fabbri, 1 ex. SMNS. – N Sichuan, valley SW Barkam, 3000–3800 m, 22.VII.1995, leg. M. Janata, 6 ex. CKBB.

Redescription: Body length 7.8–9.0 mm. Eyes (Fig. 41) not reduced, not prominent. Shape of pronotum see Fig. 41, disc with dense and partly confluent punctures, distance between 0.5–1 diameters, all punctures bearing short and adpressed setae, surface uneven, with a pair of distinct impressions on the disc and with an indistinct mediobasal impression, surface dull, lateral margins somewhat marked but unbordered, basal margin unbordered and not bent downwards, posterior angles completely rounded and indistinct, propleura with wider punctation than and similar setation as on disc. Elytra (Fig. 41) with rows of punctures without striae, punctures of rows smaller than pronotal punctures, each puncture bearing a short and adpressed seta, intervals without punctures but shagreened and dull, external intervals with a few microsetae, internal intervals flat, interval 7 distinctly convex but not keel-like, in the humeral region sometimes knob-like, external intervals with an indistinct or without any setiferous pores. All femora in both sexes without teeth.

All tibiae of males without modifications (Figs. 42–43). Aedeagus see Fig. 44.

Remarks: This species was previously only known by the holotype from Kangding (= Tatsienlu), not examined in SCHAWALLER (2001) and therefore not figured. The additional specimens were collected close to the type locality. In some specimens, the elytral interval 7 is knob-like in the humeral region and the dorsal surface is more shining, in other specimens the interval 7 is without knob-like shoulders and the dorsal surface is distinctly shagreened and dull. All other characters coincide, also the shape of the aedeagus, thus these differences are interpretated as infraspecific variations.

Laena nyingchica Schawaller, 2001

New material: E Tibet, Bomi, 3000 m, 9.–10.VII.1997, leg. M. TRÝZNA & O. ŠAFRÁNEK, 4 ex. CJTK. – E Tibet, Bomi, 3000 m, 9.–10.VII.1997, leg. J. TURNA, 1 ex. CJTK, 1 ex. SMNS. – E Tibet, road Bomi to Rawu, 30 km W Rawu, 3800 m, 11.VII.1997, leg. J. TURNA, 2 ex. CJTK, 1 ex. SMNS. – E Tibet, 25–35 km NE Nyingchi, 3300–3900 m, 30.VI.–1.VII.1996, leg. L. & R. BUSINSKÝ, 1 ex. CJTK. – E Tibet, SE Bomi, 2800 m, 6.VII.1996, leg. L. & R. BUSINSKÝ, 3 ex. CJTK. – E Tibet, N Rawu, 4200 m, 11.VII.1996, leg. L. & R. BUSINSKÝ, 3 ex. CJTK. – NW Sichuan, 20 km S Maeirma, 3800 m, 9.–29.VI.2004, leg. R. FABBRI, 3 ex. SMNS. – NW Sichuan, between Sanggarmai and Sanggarpar, 3500 m, 8.–29.VI.2004, leg. R. FABBRI, 2 ex. SMNS. – W Sichuan, W Zhier (= Zi'er), 4241 m, 5.VI.2006, leg. R. SEHNAL & M. TRÝZNA, 6 ex. BMNH.

Remarks: The above listed specimens from the Tibetian Bomi and Rawu originate close from the type locality near Nyingchi, however the other specimens from northwestern Sichuan were collected relatively far away from the Tibetian localities. The external morphology coincides in both series, only the shape and convexity of the pronotum varies in some extent between the populations.

Laena paomaica Schawaller, 2001

New material: W Sichuan, Ganzi Tibetian Autonomous Prefecture, Daxue Shan, 10 km S Kangding, 3150 m, 26.VI.1999, leg. A. PÜTZ, 4 ex. CAPE. – W Sichuan, Ganzi Tibetian Autonomous Prefecture, Daxue Shan, Mugecuo, 15 km NW Kangding, below the lowest lake, 3300 m, 27.VI.1999, leg. A. PÜTZ, 1 ex. CAPE. – W Sichuan, Ganzi Tibetian Autonomous Prefecture, 25 km NW Litang, Shaluli Shan, 4300 m, 1.VII.1999, leg. A. PÜTZ, 1 ex. CAPE. – W Sichuan, Ganzi Tibetian Autonomous Prefecture, 15 km W Yajiang, Shaluli Shan, 4300 m, 2.VII.1999, leg. A. PÜTZ, 2 ex. CAPE. – W Sichuan, Ganzi Tibetian Autonomous Prefecture, 55 km NE Batang, Shaluli Shan, 4200 m, 3.VII.1999, leg. A. PÜTZ, 1 ex. CAPE. – W Sichuan, 25 km N Jiulong, 3900 m, 13.–21.VI.2004, leg. R. FABBRI, 2 ex. SMNS. – W Sichuan, W Kangding, Zheduo Shan, 4300–4500 m, 12.–22.VI.2004, leg. R. FABBRI, 1 ex. SMNS. – S Sichuan, 30 km NW Muli (Bowa), 3500 m, 1.–2.VII.1998, leg. J. TURNA, 1 ex. CJTK. – W Sichuan, road Litang to Batang, pass 70 km WNW Litang, 4670 m, 21.–22.VII.1994, leg. J. KALÁB, 1 ex. CJTK. – SW Sichuan, pass Riwa to Lamuge, 4200 m, 28.VI.2006, leg. M. JANATA, 1 ex. BMNH.

Laena puetzi Schawaller, 2001

New material: W Sichuan, 20 km NNW Sabdé, 2000–3500 m, 18.–20.VI.1994, leg. J. KALÁB, 2 ex. CJTK. – W Sichuan, road Sabdé to Jiulong, pass 40 km N Jiulong, 24.–25.VI.1994, leg. J. KALÁB, 1 ex. CJTK, 1 ex. SMNS. – W Sichuan, Qionglai Shan, Mou Pi Shan, Barkam 15 km S Zhuokeji, 3100–3750 m, 10.–30.VI.2004, leg. R. FABBRI, 2 ex. SMNS. – NW Sichuan, 20 km W Luhua, 2750–3200 m, 8.–28.VI.2004, leg. R. FABBRI, 1 ex. SMNS. – Central Sichuan, Xuecheng Sammo, 3500 m, 1.VII.2004, leg. M. JANATA, 2 ex. BMNH. – W Sichuan, Ganzi Tibetian Autonomous Prefecture, 15 km NW Kangding, Daxue Shan, Mugecuo, 3300 m, 27.VI.1999, leg. A. PÜTZ, 1 ex. CAPE. – SW Sichuan, Yading reserve, 3750 m, 24.VI.2006, leg. M. JANATA, 1 ex. BMNH. – N Sichuan, valley SW Barkam, 3000–3800 m, 22.VI.1995, leg. M. JANATA, 8 ex. CKBB, 1 ex. SMNS. – W Sichuan, Kangding County, Gongga Shan, 3300–4800 m, 13.–19.VI.2001, leg. L. & R. BUSINSKÝ, 2 ex. CJTK.

Laena qinlingica Schawaller, 2001

New material: Shaanxi, Qinling Shan, pass on road Zhouzhi to Foping, 105 km SW Xi'an, 1990 m, 2.–4.VII.2001, leg. A. SMETANA, 3 ex. SMNS, 1 ex. CASO.

Remarks: This species possesses distinct femoral teeth as figured in the original description and as incorporated in the identification key, but in the text the femora are erroneously said to be without teeth.

Laena safraneki Schawaller, 2001

New material: N Yunnan, Baima Shan, pass 15 km SE Deqen, 4330 m, 12.VI.2005, leg. M. SCHÜLKE, 3 ex. SMNS. – N Yunnan, Deqen County, E Meili Xue Shan, 12 km SW Deqen, 2890 m, 9.VI.2005, leg. M. SCHÜLKE, 1 ex. SMNS.

Laena schuelkei Schawaller, 2001

New material: Sichuan, road between Kangding and Mugecuo, 2550–2580 m, 29.VII.–8.VIII.2006, leg. A. PUCHNER, 1 ex. CRSW.

Laena smetanai Schawaller, 2001

New material: Sichuan, road between Zhangla and Huanglong, westside, 3450–3850 m, 1.–7.VI.2006, leg. A. PUCHNER, 1 ex. CRSW.

Laena tuntalica Schawaller, 2001

New material: E Tibet, Markam, 3800–4000 m, 16.–18.VII.1996, leg. L. & R. BUSINSKÝ, 4 ex. CJTK. – E Tibet, Tuntala Shan, 40 km E Zogang, 4500 m, 29.VI.–3.VII.1997, leg. J. TURNA, 13 ex. CJTK.

Laena turnai Schawaller, 2001

New material: W Sichuan, W Zhier (= Zi'er), 4241 m, 5.VI.2006, leg. R. SEHNAL & M. TRÝZNA, 1 ex. BMNH. – Sichuan, Jinping Shan, W Mofanggou, 3350 m, 28.V.–4.VI.2005, leg. R. SEHNAL & M. TRÝZNA, 2 ex. CJTK. – SW Sichuan, NNE Eryizuxiang, 3500–3800 m, V.2004, leg. M. HÄCKEL & R. SEHNAL, 1 ex. CJTK, 1 ex. SMNS. – Sichuan, San Ya (Eryizuxiang), 3800 m, 10.VI.2005, leg. R. SEHNAL & M. TRÝZNA, 1 ex. CJTK.

Laena yajiangica Schawaller, 2001

New material: Sichuan, Ganzi Tibetian Autonomous Prefecture, 6km WSW Yajiang, Shaluli Shan, 3250m, 4.VII.1999, leg. A. Pütz, 1 ex. CAPE.

Laena yufengsi Masumoto, 1996

New material: N Yunnan, 30km N Lijiang, E Yulongxue Shan, 2800–2900m, 13.VIII.2003, leg. M. Schülke, 1 ex. SMNS. – Yunnan, pass 50km W Judian, 11.–13.VI.2005, leg. I. Jeniš, 6 ex. CJTK, 1 ex. SMNS.

Laena yuzhuensis Masumoto & Yin, 1994

New material: N Yunnan, Diancang Shan 5km SSW Dali, 2800m, 26.VIII.2003, leg. A. Smetana, 5 ex. SMNS. – N Yunnan, Diancang Shan 5km SSW Dali, 2800m, 26.VIII.2003, leg. M. Schülke, 1 ex. SMNS. – N Yunnan, Diancang Shan 5km SSW Dali, 2800m, 26.VIII.2003, leg. D. Wrase, 2 ex. CJTK.

Laena zongdianica Schawaller, 2001

New material: N Yunnan, Xue Shan near Zhongdian, 4000–4100m, 23.–24.VI.1996, leg. J. Farkač, P. Kabátek & A. Smetana, 6 ex. NHMB. – N Yunnan, 15km W Zhongdian, 3800–4200m, 22.–24.VI.1994, leg. J. Farcač & D. Král, 5 ex. NHMB. – N Yunnan, 55km N Zhongdian, 3800m, 18.VIII.2003, leg. M. Schülke, 3 ex. SMNS. – NW Yunnan/SW Sichuan border area, road Xiangcheng to Zhongdian, pass 35km S Xiangcheng, 15km N Wengshui, 3500m, 10.–13.VII.1994, leg. J. Kaláb, 2 ex. CJTK, 1 ex. SMNS. – Yunnan, Haba Shan, 3150–3500m, 7.–10.VI.2002, leg. S. Bečvář, R. & H. Fouquè, 200 ex. CRFL, 12 ex. SMNS, 4 ex. HNHM. – N Yunnan, Xue Shan 10km SW Zhongdian, 3800m, 20.VIII.2003, leg. A. Smetana, 4 ex. SMNS. – N Yunnan, 55km N Zhongdian, 3800m, 18.VIII.2003, leg. A. Smetana, 2 ex. CASO. – N Yunnan, Xue Shan near lake, 23km S Zhongdian, 3890m, 15.VI.2005, leg. A. Smetana, 1 ex. SMNS. – N Yunnan, Xue Shan near lake, 23 km S Zhongdian, 3895m, 6.VI.2005, leg. M. Schülke, 1 ex. SMNS. – N Yunnan, Xue Shan near lake, 23km S Zhongdian, 3895m, 5.–15.VI.2005, leg. D. Wrase, 9 ex. CJTK. – NW Yunnan, Haba Shan, Haba, 3200m, 2.VII.2005, leg. M. Janata, 1 ex. BMNH.

6 Key to the species of *Laena* in China

This key is a new version of the previous key compiled by Schawaller (2001), excluding the species now transferred to the genus *Hypolaenopsis* (see the separate key in chapter 3), but including the herein newly described species. The key is to be used only for identifications; it does not include all diagnostic characters, so it cannot be used for phylogenetical purposes. The key is suitable only for males because sexual characters have been used. Compare also the figures of the redescribed or newly described species by Schawaller (2001), cited in the present new key as "Sch: figs." in contrary to the new figures "Figs." in this publication. The distribution of most species is restricted to limited areas and for the identification it is helpful to compare also the distributional data. Not included in this key, as in the first version, are *Laena leonardi* Schuster, 1916 from Xinjiang/Sinkiang (belonging to the Middle Asian fauna, see Schawaller 1995), *L. ovipennis* Schuster, 1926 from nearby Hongkong (not seen) and *L.* "*chinensis*" Jingke & Peng, 1993 from the Anhui Province (see Introduction).

1 Species from the southeastern provinces Guizhou, Guangxi, Jiangxi and Fujian. **2**
– Species from the western and central provinces Xizang (= Tibet), Yunnan, Sichuan, Shaanxi, Hubei, Gansu and Henan. **6**
2 All femora with distinct teeth. **3**
– All femora without armature. **4**
3 Lateral margins of pronotum unbordered. – Figs. 1–4. . . . . ***hlavaci* n. sp.**
– Lateral margins of pronotum bordered. – Figs. 5–8. . . . . ***cooteri* n. sp.**
4 Basal margin of pronotum nearly as wide as distal margin. – Figs. 9–12. . . . . ***guangxica* n. sp.**
– Basal margin of pronotum distinctly narrower than distal margin. **5**
5 Pronotum widest anteriorly, aedeagus with triangular apicale. – Figs. 13–16. . . . . ***jiangxica* n. sp.**
– Pronotum widest in the middle, aedeagus with rounder tip of apicale. – Figs. 17–20. . . . . ***guizhouica* n. sp.**
6 Pronotum with distinctly protruding anterior corners, thus anterior pronotal margin with distinct convex excavation. . **7**
– Pronotum without protruding anterior corners, anterior pronotal margin straight or at most weakly excavated. **10**
7 Pronotal lateral margins unbordered. – Figs. 21–24. . . . . ***quinquagesima* n. sp.**
– Pronotal lateral margins bordered. **8**
8 Pronotal surface with distinct impressions, elytral intervals flat with scattered fine punctures. – Figs. 25–28. . . . . ***basumtsoica* n. sp.**
– Pronotal surface flat, without impressions, elytral intervals wrinkled with large and nearly confluent punctures. **9**
9 Body length 7.0mm, male posterior tibiae interiorly without granules, aedeagus with broad, spade-like apicale. – Figs. 29–32. . . . . ***janatai* n. sp.**
– Body length 6.0–6.5mm, male posterior tibiae interiorly with granules, aedeagus with longer apicale with knob-like tip. – Figs. 33–36. . . . . ***michaeli* n. sp.**
10 Elytral interval 7 keel-like and pronounced, lateral intervals 8 and 9 not or indistinctly visible in dorsal view, internal intervals between these keel-like intervals flat or nearly flat. **11**
– Elytral interval 7 not keel-like, sometimes interval 7 distinctly convex or sometimes intervals 3, 5 and 7 convex, but interval 7 not separating the joint elytra in a flat interior part and a vertical lateral part. **21**
11 All femora in both sexes with distinct teeth or angles. . . . **12**
– All femora in both sexes completely without armature. . . **13**
12 All femora with distinct angles but without teeth, lateral margins of pronotum unbordered and rounded. – Sch: figs. 21–24. . . . . ***kubani***
– All femora with distinct teeth, lateral margins of pronotum bordered. – Figs. 37–40. . . . . ***dabashanica* n. sp.**
13 Elytral interval 7 keel-like, swollen and knob-like in the humeral region. **14**
– Elytral interval 7 keel-like over its total length and not swollen in the humeral region. **16**
14 Joint elytra about twice as long as wide; elytra with rows of fine punctures extinguishing in the posterior part; elytral intervals dull and without setation; aedeagus with long apicale. – Figs. 41–44. . . . . ***mirabilis***
– Joint elytra about 1.6 times as long as wide; elytra with rows of large punctures; elytral intervals shining and with adpressed setation; aedeagus with broad apicale. **15**
15 Body length 8.8–9.5mm; elytral intervals wrinkled and with dense and coarse punctation; posterior tibiae of males armed with spines. – Sch: figs. 37–40. . . . . ***mulica***
– Body length 7.0–7.5mm; elytral intervals flat with fine

punctation; posterior tibiae of males without spines. – Figs. 45–48. ..... ***maowenica* n. sp.**

16 Body length 4.7–5.2 mm; lateral margins of pronotum crenulated. – Sch: figs. 33–36. ..... ***yajiangica***

– Body length over 6.0 mm; lateral margins of pronotum smooth. **17**

17 Pronotum besides impressions flat, so disc on the same level as lateral margins. **18**

– Pronotum besides impressions more or less convex, so disc higher than lateral margins. **19**

18 Base of pronotum with distinct impression (besides other impressions), this base distinctly narrower than anterior margin with protruding anterior corners; apicale of aedeagus broad, spade-like. – Sch: figs. 25–28. ..... ***yulongica***

– Base of pronotum without distinct impression, this base about as wide as anterior margin with rounded anterior corners; apicale of aedeagus longer, triangular. – Sch: figs. 29–32. ..... ***bowaica***

19 Pronotum and elytra shining; pronotum strongly convex with distinct lateral border, basal margin bent downwards; elytral rows with fine punctures. – Sch: figs. 41–44. ..... ***haigouica***

– Pronotum and elytra dull; pronotum feebly convex with marked but unbordered lateral margins, basal margin not bent downwards; elytral rows with large punctures. **20**

20 Base of pronotum distinctly narrower than anterior margin; punctures of elytral intervals as large as punctures of the rows; apicale of aedeagus triangular. – Sch: figs. 45–48. ..... ***habashanica***

– Base of pronotum about as wide as anterior margin; punctures of elytral intervals distinctly smaller than punctures of the rows; apicale of aedeagus spade-like. – Sch: figs. 49–52. ..... ***schuelkei***

21 All femora or at least anterior femora in both sexes medially with teeth or distinct angles. **22**

– All femora without distinct modifications. **48**

22 Elytra (not pronotum) without any setation in the elytral rows and intervals. **23**

– Elytra with long erect or short adpressed setae in the elytral rows and/or in the elytral intervals. **30**

23 Only anterior femora with distinct angles, middle and posterior femora without armature. – Figs. 49–52. ..... ***jinpingica* n. sp.**

– All femora with distinct teeth. **24**

24 Posterior tibiae of males without distinct modifications. . **25**

– Posterior tibiae of males with modifications (hooked interior apex or medially with tooth or dilatation). **28**

25 Lateral margins of pronotum unbordered. **26**

– Lateral margins of pronotum bordered. **27**

26 Body length 6.2–7.5 mm, aedeagus with longer apicale with rounded finger-like tip. – Sch: figs. 65–68. ..... ***smetanai***

– Body length 7.5–8.5 mm, aedeagus with broad apicale with blunt tip. – Figs. 53–56. ..... ***bohrni* n. sp.**

27 Basal margin of pronotum distinctly narrower than distal margin, pronotum cordiform; aedeagus with longer triangular apicale; anterior femora of males of similar size as middle and posterior femora, anterior femora besides hook-like tooth with rounded anterior corner. – Sch: figs. 53–56. ..... ***chinensis***

– Basal margin of pronotum as wide as distal margin, pronotum subquadrate; aedeagus with broader spade-like apicale; anterior femora of males extraordinary thick and besides broad tooth with additional tooth-like anterior corner. – Figs. 57–60. ..... ***sehnali* n. sp.**

28 Posterior tibiae of males with distinctly hooked inner apex, medial side with granules; apicale of aedeagus about twice as long as wide. – Sch: figs. 57–60. ..... ***turnai***

– Posterior tibiae of males medially dilatated or with teeth, without granules; apicale of aedeagus subquadrate. **29**

29 Elytral intervals with distinct punctation; male anterior tibiae with parallel inner side; male posterior tibiae medially with tooth. – Sch: figs. 61–64. ..... ***tabanai***

– Elytral intervals only with very fine and scattered punctures; male anterior tibiae medially with dilatation; male posterior tibiae medially with rounded dilatation. – Sch: figs. 69–72. ..... ***hubeica***

30 Only anterior femora with teeth, medial and posterior tibiae without modifications. – Sch: figs. 73–76. ..... ***yasuakii***

– All femora with teeth or at least with distinct angles. ... **31**

31 Body length 9.3–9.6 mm; elytra with dense and large punctation of the intervals, so the elytral intervals are indistinct. – Sch: figs. 77–80. ..... ***shaluica***

– Body length less than 8.0 mm; elytra with distinct elytral rows and separated intervals. **32**

32 Lateral margins of pronotum distinctly bordered. **33**

– Lateral margins of pronotum unbordered, sometimes feebly marked. **36**

33 Eyes prominent; pronotum cordiform with the basal margin distinctly narrower than anterior margin; body length 6.6–7.9 mm. – Sch: figs. 85–88. ..... ***angulifemoralis***

– Eyes not prominent; pronotum subquadrate with the basal margin as wide as the anterior margin; body length 3.5–6.0 mm. **34**

34 Pronotum and elytra with erect and long setation; apicale of aedeagus short and broad. – Sch: figs. 97–100. ... ***luguica***

– Pronotum and elytra with short and adpressed setation; apicale of aedeagus long and triangular. **35**

35 Pronotum widest in the middle. – Sch: figs. 101–104. – SW Tibet. ..... ***formaneki***

– Pronotum widest near the anterior corners. – Figs. 61–64. – N Yunnan. ..... ***farkaci* n. sp.**

36 Pronotum with coarse, partly confluent punctation, surface of pronotum wrinkled or uneven. **37**

– Pronotum with fine punctation, punctures always distinctly separated, surface of pronotum smooth. **40**

37 Odd-numbered elytral intervals distinctly convex; all femora with distinct teeth. – Sch: figs. 121–124. ..... ***ganzica***

– All elytral intervals homogeneous, either all slightly convex or all flat; femora only with angles, the latter partly reduced. **38**

38 Pronotum subquadrate with the basal margin as wide as the anterior margin; male anterior tibiae medially with distinct tooth. – Sch: figs. 117–120. ..... ***ludingica***

– Pronotum cordiform with the basal margin narrower than the anterior margin; male anterior tibiae without modification. **39**

39 Elytral intervals densely scattered with large and confluent punctures; aedeagus with broad apicale with blunt tip. – Sch: figs. 105–108. ..... ***jizushana***

– Elytral intervals with a row of separated small punctures; aedeagus with triangular apicale. – Sch: figs. 125–128. ..... ***yufengsi***

40 Pronotum and elytra with dull shagreened surface and with long, dense and erect setation. – Sch: figs. 109–112. ..... ***qinlingica***

– Pronotum and elytra with shining surface and with sparser short and adpressed setation. **41**

41 Pronotum with fine and sparse punctation; pronotal punctures distinctly smaller than punctures of the elytral rows. – Figs. 65–68. ..... ***lisuorum* n. sp.**

– Pronotum with larger punctures, which are of similar size as those of the elytral rows. **42**

42 Pronotum cordiform, basal margin distinctly narrower than anterior margin. **43**

– Pronotum either subquadrate or trapezoid, basal margin as wide as or only slightly narrower than anterior margin... **44**

43 Joint elytra oval; aedeagus with longer triangular apicale. – Sch: figs. 81–84. ..... ***wolongica***

– Joint elytra longer and parallel; aedeagus with broad apicale with blunt tip. – Figs. 69–72. ..... ***barkamica* n. sp.**

44 Pronotum widest in the middle. **45**

– Pronotum widest before the middle (three quite similar species, compare body length, dorsal punctation, setation and shape of aedeagus and distribution). **46**

45 Body length 3.7–3.8 mm; posterior tibiae of males only with finely hooked interior apex; aedeagus with longer triangular apicale. – Sch: figs. 93–96. ..... ***daxueica***

– Body length 5.0 mm; posterior tibiae of males with finely hooked interior apex and medially swollen in the middle; aedeagus with broader apicale with blunt apex. – Sch: figs. 113–116. ..... ***cylindrica***

46 Body length above 5.5 mm. – Shaanxi and N Sichuan. – Sch: figs. 129–132. ..... ***fengileana***

– Body length 3.0–4.2 mm. – S Tibet and Yunnan. **47**

47 Punctures of elytral intervals smaller than pronotal punctures; punctures of elytral rows without setae, only elytral intervals with setae – S Tibet. – Sch: figs. 89–92. . .***gracilis***

– Punctures of elytral rows equal in size to pronotal punctures, each puncture bearing a seta, intervals with a row of fine punctures bearing a similar seta. – Yunnan. – Figs. 73–76. . ..... ***septuagesima* n. sp.**

48 Small species (4.2–6.0 mm) with distinctly dull surface and pronotum with coarse and confluent punctation. **49**

– Small and large species; if body length below 6.0 mm then with shining surface and pronotum with separated punctation. **50**

49 Elytral intervals 3, 5 and 7 distinctly but equally convex, other elytral intervals flat; lateral margins of pronotum marked and crenulated but unbordered; aedeagus with longer triangular apicale. – Figs. 77–80. ..... ***davidi* n. sp.**

– Elytral intervals 3 and 5 slightly, 7 distinctly convex, intervals with rows of distinct granules; lateral margins of pronotum not bordered and not marked; aedeagus with broad spade-like apicale. – Figs. 81–84. ..... ***gaoligongica* n. sp.**

50 Elytra (not pronotum) without any setation or with very short setation in the elytral rows and/or intervals (setae not distinctly longer than a diameter of the punctures in the rows). **51**

– Elytra with distinct, adpressed shorter or erect longer setation in the elytral rows and/or intervals. **79**

51 Punctation of elytra confused, surface not distinctly separated in elytral rows and intervals. **52**

– Elytra always with distinct elytral rows and punctate or impunctate intervals, sometimes punctures in the intervals as large as in the rows, sometimes the elytral rows extinguished in the posterior part of the elytra. **54**

52 Body length 5.5–6.2 mm; punctation on pronotum and elytra distinctly separated, surface shining. – Sch: figs. 133–135. . ..... ***heinzi***

– Body length 6.5–8.0 mm; punctation on pronotum and elytra confluent, surface dull. **53**

53 Pronotum distinctly broader than long; elytra 1.5 times as long as wide, widest in posterior third. – Sch: figs. 140–143. ..... ***businskyorum***

– Pronotum nearly as wide as long; elytra 1.8 times as long as wide, widest in the middle; few differences, but no intermediate forms known. – Sch: figs. 144–147. ..... ***deqenica***

54 Elytral intervals besides the puncture rows with distinct punctation, these punctures densely scattered and about half as large as punctures in the rows. – Sch: figs. 136–139. . . . . ***safraneki***

– Elytral intervals between the puncture rows without distinct punctation or only with an indistinct row of very fine punctures. **55**

55 Small species (4.4–6.6 mm) from Tibet with a flat and subquadrate pronotum, pronotal disc smooth and without impressions, lateral pronotal margin bordered. **56**

– Smaller and larger species with different structure of the pronotum; if with similar pronotum than not from Tibet, if from Tibet than with a different pronotum. **59**

56 Male tibiae without secondary sexual characters. **57**

– Anterior and/or posterior male tibiae with secondary sexual characters. **58**

57 Pronotum with rounded lateral margins; elytral punctures larger, distance sometimes only about 1 diameter. – Sch: figs. 164–167. ..... ***alticola***

– Pronotum with parallel lateral margins; elytral punctures finer, distance always over 2 diameters; few differences, but no intermediate forms known. – Sch: figs. 168–171. ..... ***parallelocollis***

58 Anterior and posterior tibiae of males swollen medially; apicale of aedeagus broad with blunt tip. – Sch: figs. 156–159. ..... ***tuntalica***

– Anterior tibiae of males slightly excavated medially; apicale of aedeagus narrower and triangular. – Sch: figs. 200–203. ..... ***cholanica***

59 Large species (7.8–10.3 mm) with long and parallel elytra, with a flat subquadrate pronotum with bordered lateral margins, and with a row of distinct spines interiorly in the distal half of the male posterior tibiae. **60**

– Larger or smaller species with a different combination of these characters. **63**

60 Pronotum about 1.1–1.3 times as broad as long; apicale of aedeagus broad and with blunt tip. **61**

– Pronotum about as wide as long; apicale of aedeagus triangular. **62**

61 Pronotum widest before the middle; male anterior tibiae without modification. – Sch: figs. 180–183. ..... ***tryznai***

– Pronotum widest behind the middle; male anterior tibiae medially excavated. – Figs. 85–88. ..... ***kalabi* n. sp.**

62 Pronotum with parallel sides; posterior tibiae of males besides spines distally somewhat swollen but without distinctly hooked inner apex. – Sch: figs. 176–179. ..... ***dickorei***

– Pronotum with rounded sides; posterior tibiae of males besides spines distally somewhat swollen and with distinctly hooked inner apex. – Sch: figs. 172–175. ..... ***gyamdaica***

63 Lateral margins of pronotum completely unbordered and also not marked. **64**

– Lateral margins of pronotum completely or at least partly bordered. **66**

64 Small body size (3.8–4.8 mm); pronotum cordiform, basal margin distinctly narrower than anterior margin. – Sch: figs. 148–151. ..... ***diancangica***

– Body medium-sized (6.5–8.8 mm); pronotum round. . . . **65**

65 Anterior tibiae of males medially with a distinct tooth; joint elytra of oval shape. – Sch: figs. 188–191. ..... ***schusteri***

– Anterior tibiae of males without modification; joint elytra long and parallel. – Sch: figs. 160–163. ..... ***hengduanica***

66 Posterior tibiae of males medially with a distinct hump-like dilatation shortly before apex. – Sch: figs. 192–195. ..... ***baishuica***

– Posterior tibiae of males with different modification or without secondary sexual characters. **67**

67 Posterior tibiae of males medially with a single spine shortly before apex. – Figs. 89–92. ..... ***naxiorum* n. sp.**

– Posterior tibiae of males with different modification or without secondary sexual characters. **68**

68 All tibiae in male without distinct modifications. **69**

– Anterior and/or posterior tibiae in male modified. **73**

69 Basal margin of pronotum distinctly narrower than anterior margin, pronotum cordiform. **70**

– Pronotum broad, subquadrate or round, basal margin not distinctly narrower than anterior margin. **71**

70 Body length 4.6 mm; aedeagus with long triangular apicale. – Sch: figs. 152–155. . . . . ***zogqenica***

– Body length 6.0–8.5 mm; aedeagus with spade-like apicale with blunt tip. – Figs. 93–96. . . . . ***fouquei* n. sp.**

71 Pronotum flat and subquadrate. **72**

– Pronotum convex and round. – Sch: figs. 196–199. . . . . ***langmusica***

72 Pronotum with large but sparse punctation; aedeagus with triangular apicale with acute tip. – Figs. 97–100. . . . . ***alesi* n. sp.**

– Pronotum with fine but dense punctation; aedeagus with spade-like apicale with blunt tip. – Sch: figs. 216–219. . . . . ***nyingchica***

73 Elytral rows distinctly distinguished in the posterior part of the elytra; elytral intervals distinctly shagreened and dull. – Sch: figs. 204–207. . . . . ***xuerensis***

– Elytral rows more or less complete; elytral intervals shining. **74**

74 Pronotum cordiform, its base distinctly narrower than anterior margin.. . . . . **75**

– Pronotum r ound or subquadrate, its base more or less as wide as anterior margin. **76**

75 Body length 10.0–11.5 mm; elytra with rows of punctures in distinct striae; posterior tibiae of males swollen interiorly in the middle; apicale of aedeagus thin and finger-like. – Sch: figs. 184–187. . . . . ***gigantea***

– Body length 8.0–9.0 mm; elytra with rows of punctures without striae; posterior tibiae of males swollen interiorly at base; apicale of aedeagus broad spade-like. – Figs. 101–104. . . . . ***baiorum* n. sp.**

76 Basal margin of pronotum bent downwards, so this margin is on a distinctly deeper level than disc. – Sch: figs. 208–211. . . . . ***kangdingica***

– Basal margin of pronotum not bent downwards, so this margin is more or less on the same level as disc. **77**

77 All tibiae of males with a few indistinct granules at the inner side, but without excavations or dilatations; body length in the average smaller (4.5–6.5 mm). – Figs. 109–112. . . . . ***xueshanica* n. sp.**

– Anterior tibiae of males interiorly with excavation, posterior tibiae interiorly swollen or with hooked apex. **78**

78 Pronotum round; posterior tibiae of males interiorly with hooked apex; apicale of aedeagus longer spade-like. – Sch: figs. 212–215. . . . . ***zongdianica***

– Pronotum subquadrate; posterior tibiae of males interiorly with dilatation in the distal part; apicale of aedeagus very short and broad. – Figs. 105–108. . . . . ***nujiangica* n. sp.**

79 Eyes prominent; posterior tibiae of males medially swollen and interiorly with hooked apex. – Figs. 113–116. . . . . ***baoshanica* n. sp.**

– Eyes not prominent; posterior tibiae of males either differently modified or completely unmodified. **80**

80 Elytral intervals between elytral rows either with distinct scattered punctures or with an additional row of large punctures (interval punctures about half as large as punctures of the rows). **81**

– Elytral intervals without or only with a row of indistinct very fine punctures in the elytral intervals. **84**

81 Elytral intervals with a single row of distinct punctures; posterior tibiae of males medially granulated. – Sch: figs. 220–223. . . . . ***becvari***

– Elytral intervals with scattered dense and large punctation. **82**

82 Posterior tibiae of males medially with a distinct tooth; apicale of aedeagus broad and spade-like. – Sch: figs. 224–227. . . . . ***houzhenzica***

– Posterior tibiae of males only with finely hooked inner apex; apicale of aedeagus longer and triangular. **83**

83 Pronotum and elytra dull, punctation of pronotum confluent; anterior femora of males medially granulated; anterior tibiae of males with a hooked inner apex. – Sch: figs. 231–234. . . . . ***bifoveolata***

– Pronotum and elytra shining, punctation of pronotum separated; anterior femora of males smooth; anterior tibiae of males distinctly swollen medially. – Sch: figs. 235–238. . . . . ***puetzi***

84 Pronotum and elytra with long and erect setae. **85**

– Pronotum and elytra with short, adpressed setae. **88**

85 Pronotum with rounded lateral margins, widest in the middle; base of pronotum indistinctly bordered and bent downwards; pronotum with fine punctation, these punctures distinctly finer than punctures in the elytral rows. – Sch: figs. 228–230. . . . . ***hingstoni***

– Pronotum subquadrate or long trapezoid, widest before middle; base of pronotum unbordered and not bent downwards; pronotum with larger punctures of same size as punctures in the elytral rows. **86**

86 Pronotum long, trapezoid; elytra longer and parallel. – Sichuan. – Figs. 117–120. . . . . ***moxica* n. sp.**

– Pronotum subquadrate; elytra shorter and oval. – Yunnan. **87**

87 Apicale of aedeagus triangular with sinuated lateral margins and finger-like tip. – Sch: figs. 239–242.. . . . . ***watanabei***

– Apicale of aedeagus broad with blunt tip. – Sch: figs. 243–246. . . . . ***daliensis***

88 Pronotum with coarse punctation, punctures often confluent, disc with distinct impressions, surface dull and shagreened. **89**

– Pronotum with finer punctation, punctures never confluent, disc without impressions, surface shining. **91**

89 Anterior margin of pronotum excavated and anterior corners protruding, lateral margins distinctly bordered. – Sch: figs. 247–250. . . . . ***yuzhuensis***

– Anterior corners of pronotum not distinctly protruding, lateral margins unbordered or at least indistinctly marked. . **90**

90 Elytral inner intervals flat, intervals 5 and 7 convex; intervals about 3 times as wide as the punctures of the elytral rows; setae of elytral intervals distinctly longer than setae of the rows. – Sch: figs. 251–254. . . . . ***luhuoica***

– Elytral intervals equally convex; intervals about 1–2 times as wide as the punctures of the elytral rows; setae of elytral intervals as long as setae of the rows. – Sch: figs. 259–262. . . . . ***wrasei***

91 Pronotum widest in the anterior third, lateral margins bordered. **92**

– Pronotum widest in the middle, lateral margins unbordered. **93**

92 Elytral intervals with a row of fine punctures bearing short adpressed setae; elytra longer and parallel. – Sichuan. – Sch: figs. 255–258. . . . . ***paomaica***

– Elytral intervals scattered with dense fine punctation, punctures bearing longer adpressed setae; elytra shorter and oval. – Yunnan. – Figs. 121–124. . . . . ***gyalthangica* n. sp.**

93 Apicale of aedeagus triangular with straight sides and with acute tip. – Sch: figs. 263–266. . . . . ***brendelli***

– Apicale of aedeagus broad with sinuated sides and blunt tip. – Sch: figs. 267–270. . . . . ***emeishana***

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Manuscript received: 1.III.2007, accepted: 25.IV.2007.

The species of *Platydema* Laporte & Brullé (Coleoptera: Tenebrionidae) from New Guinea and the Moluccan Islands, with descriptions of 11 new species[1]

Wolfgang Schawaller

Abstract

The species of the genus *Platydema* Laporte & Brullé, 1831 (Coleoptera: Tenebrionidae: Diaperini) from New Guinea and the Moluccan Islands are revised. The diagnostic characters are figured, a species key for all 27 species is compiled. – New species: *Platydema bacanicum* **n. sp.**, *P. cyclopsicum* **n. sp.**, *P. djuremnaicum* **n. sp.**, *P. halmahericum* **n. sp.**, *P. kaiense* **n. sp.**, *P. papuanum* **n. sp.**, *P. pseudofuligineum* **n. sp.**, *P. seramicum* **n. sp.**, *P. skalei* **n. sp.**, *P. wamenaicum* **n. sp.**, *P. weigeli* **n. sp.** – New synonym: *Platydema gebieni* Kaszab, 1939 **n. syn.** = *Platydema striolatum* Kaszab, 1939. – New combination: *Platydema confusum* (Kaszab, 1939) **n. comb.** from *Alphitophagus*. – Lectotype designations are given for *Alphitophagus confusus* Kaszab, 1939, *Platydema biroi* Kaszab, 1939, *P. denticapitis* Kaszab, 1939, *P. gebieni* Kaszab, 1939, *P. globigerum* Kaszab, 1939, and *P. hastatum* Kaszab, 1939.

Keywords: Coleoptera, Tenebrionidae, Diaperini, *Platydema*, New Guinea, Moluccan Islands, new species, taxonomy, species key.

Zusammenfassung

Die Arten der Gattung *Platydema* Laporte & Brullé, 1831 (Coleoptera: Tenebrionidae: Diaperini) von Neu Guinea und den Molukken werden revidiert. Die diagnostischen Merkmale werden abgebildet, ein Bestimmungsschlüssel für alle 27 Arten wird aufgestellt. – Neue Arten: *Platydema bacanicum* **n. sp.**, *P. cyclopsicum* **n. sp.**, *P. djuremnaicum* **n. sp.**, *P. halmahericum* **n. sp.**, *P. kaiense* **n. sp.**, *P. papuanum* **n. sp.**, *P. pseudofuligineum* **n. sp.**, *P. seramicum* **n. sp.**, *P. skalei* **n. sp.**, *P. wamenaicum* **n. sp.**, *P. weigeli* **n. sp.** – Neues Synonym: *Platydema gebieni* Kaszab, 1939 **n. syn.** = *Platydema striolatum* Kaszab, 1939. – Neue Kombination: *Platydema confusum* (Kaszab, 1939) **n. comb.** von *Alphitophagus*. – Lectotypen werden festgelegt für *Alphitophagus confusus* Kaszab, 1939, *Platydema biroi* Kaszab, 1939, *P. denticapitis* Kaszab, 1939, *P. gebieni* Kaszab, 1939, *P. globigerum* Kaszab, 1939 und *P. hastatum* Kaszab, 1939.

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1 Introduction

In continuation of my previous contributions on the taxonomy and distribution of species of the genus *Platydema* Laporte & Brullé, 1831 (Schawaller 2003, 2004a, 2004b) the present paper deals with the 27 species (including 11 new species) known from New Guinea including small adjacent islands (Japen, Salawati, Biak, Batanta) and from the Moluccan Islands (major islands Halmahera, Seram, Buru, Ambon, Ternate, Aru Islands, Kai Islands) (Fig. 1). Species occuring exclusively on the Pacific Islands are not considered here, and all species (except *P. fuligineum* for comparative purposes) described from Australia are not included as well, although biogeographic relationships may exist. The terms New Guinea and the Moluccan Islands are used in a physical geographical sense (the Moluccan Islands and West Papua belong politically to Indonesia, the eastern Papua New Guinea is an independent state).

The treated species have been described in various papers (Champion 1893; Gebien 1922, 1925; Kaszab 1939; Kulzer 1957) and have never been revised in a comprehensive way. The species characters within the genus have been discussed in my previous contributions (Schawaller, 2003, 2004a, 2004b). All species are adapted to fungal habitats and may be considered as one of the indicator species for mature forests, which are endangered worldwide.

The distributional data in this paper are not just collected from the labels alone but are partly completed by additional data for a better localization and translated in

[1] Contributions to Tenebrionidae, no. 70. – For no. 69 see Stuttgarter Beiträge zur Naturkunde A, N. S. 1: 387–411 (2008).

Fig. 1. The investigated area of New Guinea including small adjacent islands with records of *Platydema* (Biak, Japen, Waigeo, Salawati, Batanta) and the Moluccan Islands (Halmahera, Bacan, Seram, Ambon, Damar, Aru, Kai).

several cases from other languages into English. The old German colonial names have been listed (in quotation marks), when no recent locality name was available. The Indonesian (western) part of New Guinea is listed herein consequently as West Papua, even if older specimens are labelled with Irian Jaya. Specimens from the Indonesian provinces Maluku and/or Maluku Utara, even if labelled so, are listed herein consequently under Moluccan Islands.

In all cases, in which the original descriptions are based on an unspecified number of syntypes (independent from the labelling), lectotypes are designated herein in order to fix a single name-bearing type and thus to define the species, according to Article 74.7.3 of the International Code of Zoological Nomenclature.

Acronyms of depositories

BMNH The Natural History Museum, London (Max Barclay)
CASH Collection André Skale, Hof/Saale
CKAO Collection Dr. Kiyoshi Ando, Osaka
CRGT Collection Dr. Roland Grimm, Tübingen
HNHM Hungarian Natural History Museum, Budapest (Dr. Ottó Merkl)
NME Naturkundemuseum, Erfurt (Matthias Hartmann)
SMNS Staatliches Museum für Naturkunde, Stuttgart
ZSM Zoologische Staatssammlung, München (Dr. Martin Baehr, Prof. Dr. H. J. Bremer)

Acknowledgements

Cordial thanks are due to Dr. Kiyoshi Ando (Osaka), Dr. Martin Baehr (München), Max Barclay (London), Prof. Dr. H. J. Bremer (Melle), Dr. Roland Grimm (Tübingen), Matthias Hartmann (Erfurt) and Dr. Ottó Merkl (Budapest) for the loan of specimens under their care. Dr. Alexander Riedel (Karlsruhe) kindly deposited huge collections of beetles, and not only tenebrionids, from New Guinea in the Natural History Museum Stuttgart. Furthermore, I am grateful to Dr. Ottó Merkl and an anonymous reviewer for critically reading the manuscript.

The photographs were taken by Johannes Reibnitz (Stuttgart) with a Leica DFC320 digital camera on a Leica MZ16 APO microscope and subsequently processed by him with Auto-Montage (Syncroscopy) software. He also scanned my drawings and mounted them on plates.

2 The previously known Papuan and Moluccan species of *Platydema*

Platydema asymmetricum Champion, 1893 (Figs. 21, 77–79)

New material: Damma Island, leg. J. J. Walker, 7 ex. BMNH (topotypic specimens but not labelled as types; specimens labelled as types not present in BMNH). – Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, 1899, leg. L. Biró, 1 ex. HNHM. – Papua New Guinea, Prov. Morobe, Kaiapit, XII.1978, leg. W. G. Ullrich, 1 ex. ZSM. – Papua New Guinea, Kiunga, 23.VII.–2.VIII.1969, leg. J. Balogh, 1 ex. HNHM. – West Papua, Prov. Paniai, Epomani, km 145, 550–750 m, 15.–16.I.1996, leg. A. Riedel, 2 ex. ZSM. – West Papua, Japen Island, Kontiunai, 600–700 m, 23.XII.2000, leg. A. Riedel, 2 ex. SMNS. – West Papua, Prov. Raja Ampat, Salawati Island, Kaliam, 22.I.2004, leg. A. Weigel, 2 ex. NME, 2 ex. CRGT. – Solomon Islands, Ysabel Island, Rasa, 20.VIII.1963, leg. P. Greenslade, 5 ex. BMNH, 1 ex. SMNS.

Distribution: Damar (= Damma) Island NE of Timor (type locality), New Guinea (KASZAB 1939), Solomon Islands (new record).

Platydema biroi Kaszab, 1939
(Figs. 17, 65–67)

Studied type material: Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, 1899, leg. L. BIRÓ, ♂ "type" HNHM, designated herewith as lectotype. – Same data as before, 1 ♂ "cotype", now paralectotype.

New material: Papua New Guinea, Prov. Morobe, Kaiapit, XII.1978, leg. W. G. ULLRICH, 1 ex. SMNS. – Papua New Guinea, Prov. Morobe, Wau, Ecological Station, 11.XI.1988, leg. R. HOLYNSKI, 1 ♀ HNHM (identification of female doubtful).

Distribution: New Guinea (type locality "Sattelberg").

Platydema confusum (Kaszab, 1939) **n. comb.**
(Figs. 5, 33–35)

Alphitophagus confusus Kaszab, 1939.

Studied type material: Papua New Guinea, Simbang, Huon Golf, 1899, leg. L. BIRÓ, ♂ "type" of *Alphitophagus confusus* HNHM, designated herewith as lectotype. – Papua New Guinea, Idenburg River, Prauvenbivak, 1920, leg. W. C. VON HEURN, 1 "cotype" HNHM, now paralectotype.

New material: Papua New Guinea, Port Moresby, Brown River, 17.–18.VIII.1968, leg. I. LOKSA, 2 ex. HNHM, 1 ex. SMNS. – Papua New Guinea, Port Moresby, 4.–18.IV.1983, leg. M. HOLYNSKA, 1 ex. HNHM. – Papua New Guinea, Kokoda, 1200 ft., VIII.1933, leg. L. E. CHEESMAN, 3 ex. BMNH.

New combination: The species was described by KASZAB (1939) as *Alphitophagus confusus*, but it shares all characters of *Platydema*. The type series in the collection of the HNHM was already labelled as *Platydema* and consequently transferred to this genus by the late Dr. KASZAB.

Distribution: New Guinea (type locality Simbang).

Platydema denticapitis Kaszab, 1939
(Figs. 16, 62–64)

Studied type material: Papua New Guinea, Erima, Astrolabe Bay, 1897, leg. L. BIRÓ, ♂ "type" HNHM, designated herewith as lectotype. – Same data, ♀ "type", 1 ♀ "cotype" HNHM, now paralectotypes. – Papua New Guinea, "Stephansort", Astrolabe Bay, 1898, leg. L. BIRÓ, 1 ♂ "cotype" HNHM, now paralectotype.

New material: Papua New Guinea, Mt. Lamington, 1300–1500 ft., leg. C. T. MCNAMARA, 2 ex. BMNH. – Papua New Guinea, Kiunga, 23.VII.–2.VIII.1969, leg. J. BALOGH, 4 ex. HNHM. – Papua New Guinea, Prov. New Ireland, Hans Meyer Range, 60 km SE Namatanai, Hirudan River, 50 m, 9.III.2000, leg. A. WEIGEL, 1 ex CRGT. – West Papua, Jayapura, Sentani, Cyclops Mts., 300 m, 9.–11.VIII.1991, leg. A. RIEDEL, 7 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 300–450 m, 8.VIII.1992, leg. A. RIEDEL, 17 ex. SMNS, 2 ex. CKAO. – West Papua, Jayapura, Sentani, Cyclops Mts., 400–800 m, 7.VIII.1992, leg. A. RIEDEL, 2 ex. SMNS. – West Papua, Baliem Distr., Kangime, 1400–1700 m, 4.IX.1990, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, Manokwari, Gunung Meja, 200 m, 30.XII.2000, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, 120 km S Nabire, Unipo-Ebore, 500 m, 4.I.1996, leg. A. WEIGEL, 1 ex. CRGT.

Distribution: New Guinea (type locality Erima).

Platydema detersum Walker, 1858

New material: Moluccan Islands, Seram, 12 km SE Wahai, Solea, 17.I.–6.II.1997, leg. S. BILÝ, 1 ex. ZSM. – Papua New Guinea, Madang Distr., Finisterre Mts., Moro, 5550 ft., 30.X.–15.XI.1964, leg. M. E. BACCHUS, 1 ex. BMNH. – Papua New Guinea, E Highland Distr., Okapa, 5000 ft., 4.–15.II.1965, leg. M. E. BACCHUS, 2 ex. BMNH. – Papua New Guinea, Wau, Bishop Museum Field Station, 15.–25.IV.1965, leg. J. BALOGH & J. SZENT-IVÁNY, 7 ex. HNHM. – Papua New Guinea, Prov. Morobe, Aseki, 1000–1300 m, 13.X.1992, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, Fak Fak, 2 km E airstrip, 16.–18.VII.1996, leg. P. SCHÜLE & P. STÜBEN, 1 ex. SMNS. – West Papua, Paniai, Mulia, Wuyuneeri, 1900–2200 m, 6.–7.VII.1994, leg. A. RIEDEL, 2 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 300 m, 19.–21.IX.1990, leg. A. RIEDEL, 6 ex. SMNS. – West Papua, Manokwari, Ransiki, Mayuby, 26.–30.IX.1990, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, Testega, 1200 m, 31.III.–12.IV.1993, leg. A. RIEDEL, 2 ex. SMNS. – West Papua, Wandammen Bay, Wasior, 100–200 m, 7.–9.I.2001, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, Biak Island, Korim, Roidifu, 100 m, 2.II.2001, leg. A. RIEDEL, 1 ex. SMNS. – West Papua, Biak Island, Korim, Nernu, 100–150 m, 1.–4.II.2001, leg. A. RIEDEL, 2 ex. SMNS. – West Papua, Biak Island, 10 km N Bosnik, 13.II.1998, leg. A. WEIGEL, 1 ex. CRGT. – West Papua, Japen Island, 20 km E Serui, 2.–5.I.1999, leg. A. WEIGEL, 1 ex. NME, 1 ex. CRGT. – West Papua, 170 km S Nabire, Epomani, 1150 m, 6.I.1996, leg. A. WEIGEL, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Salawati Island, Kaliam, 21.–24.I.2004, leg. A. SKALE, 2 ex. NME, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Batanta Island, Waywesar, 18.I.2004, leg. A. WEIGEL, 1 ex. NME.

Remarks: Figured by SCHAWALLER (2003).

Distribution: Widespread in SE Asia, Philippines, New Guinea (GEBIEN 1922 under synonym *Platydema laticorne* Fairmaire, 1882), Moluccan Islands (new record), Renell Island, Australia.

Platydema furcaticorne Gebien, 1925
(Fig. 7)

New material: Moluccan Islands, Kai (= Key) Island, 1 ♀ HNHM. – West Papua, Prov. Paniai, Epomani, km 145, 550–750 m, 15.–16.I.1996, leg. A. RIEDEL, 1 ♂ SMNS.

Remarks: The identification of the above mentioned female is not quite sure, because the characteristic shape of the male head with two long and narrow horns (GEBIEN 1925: pl. 1, fig. 8) cannot be compared. The colour pattern of the elytra with a single yellow transverse band coincides with the pattern of the holotype (GEBIEN 1925: pl. 1, fig. 9). The aedeagus of this species is still unknown (the above listed male is not figured because it was added during proof). The elytral colour pattern is identical with that of *Platydema halmahericum* n. sp., however this species has an unarmed male head.

Distribution: Moluccan Islands (type locality Aru Islands), New Guinea.

Platydema globigerum Kaszab, 1939
(Figs. 15, 59–61)

Studied type material: Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, 1899, leg. L. Biró, ♂ "cotype" HNHM, designated herewith as lectotype. – Same data, 1 ♀ "cotype" HNHM, now paralectotype.

Distribution: New Guinea (type locality "Sattelberg").

Platydema hastatum Kaszab, 1939
(Figs. 18, 68–70)

Studied type material: Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, 1899, leg. L. Biró, ♂ "type" HNHM, designated herewith as lectotype (aedeagus fragmentary). – Same data, 1 ♀ "type", 1 ♀ HNHM, now paralectotypes.

New material: Papua New Guinea, Prov. Morobe, 10 km S Garaina, Saureri, 1800–2150 m, 26.III.1998, leg. A. Riedel, 4 ex. ZSM, 1 ex. SMNS. – West Papua, Jayawijaya, Emdoman, 900–1200 m, 29.IX.1993, leg. A. Riedel, 1 ♀ SMNS. – West Papua, Merauke, Senggo, trail to Abau, 100 m, 15.–17. VI.1994, leg. A. Riedel, 1 ♂ SMNS. – West Papua, Prov. Manokwari, Membey, 800–1200 m, 31.VIII.1991, leg. A. Riedel, 2 ♀♀ SMNS. – West Papua, 47 km S Kwatisore, Urie Camp, E Nabrie, 5.III.1998, leg. A. Weigel, 1 ♀ CRGT.

Distribution: New Guinea (type locality "Sattelberg").

Platydema novaeguineense Gebien, 1922
(Figs. 8, 39–41)

New material: Papua New Guinea, "Friedrich-Wilhelmshafen" (= Madang), without date, 1 ex. HNHM. – Papua New Guinea, Prov. Morobe, Gurakor, XII.1979, leg. W. G. Ullrich, 1 ex. CKAO. – West Papua, Jayapura, Sentani, Cyclops Mts., 300 m, 19.–21.IX.1990, leg. A. Riedel, 6 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 300–500 m, 31.X.1992, leg. A. Riedel, 1 ex. SMNS. – West Papua, Baliem Distr., Kangime, 1400–1700 m, 4.IX.1990, leg. A. Riedel, 1 ex. SMNS. – West Papua, Manokwari, Gunung Meja, 200 m, 30.XII.2000, leg. A. Riedel, 1 ex. SMNS. – West Papua, Prov. Manokwari, 6 km N Manokwari, Desa Pami, 100 m, 9.III.2007, leg. A. Skale, 2 ex. CASH. – West Papua, Wandammen Bay, Wondiwoi Mts., Wasior, 250–600 m, 4.I.2001, leg. A. Riedel, 2 ex. SMNS. – West Papua, Fak Fak Distr., Yamur lake area, 100 m, IV.1998, leg. M. Balke, 1 ex. NME, 1 ex. CRGT. – West Papua, 120 km S Nabire, Unipo-Ebore, 500 m, 4.I.1996, leg. A. Weigel, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Batanta Island, Wallebet, 18.–21.I.2004, leg. A. Skale, 1 ex. NME, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Batanta Island, Yensawai, 16.I.2004, leg. A. Weigel, 1 ex. CRGT. – Solomon Islands, Ysabel Island, 1.III.1962 and 20.VIII.1963, leg. P. Greenslade, 2 ex. BMNH.

Distribution: New Guinea (type locality Doré), Solomon Islands (new record).

Platydema pallidicolle Lewis, 1894

New material: Moluccan Islands, Halmahera, Buli, Maba, 50–650 m, 8.XI.1999, leg. A. Riedel, 2 ex. SMNS. – Moluccan Islands, Ambon, 20 m, 16.II.1961, leg. A. M. R. Wegner, 1 ex. HNHM. – Moluccan Islands, Seram, Air Besar 6 km E Wahai, 5.XI.1998, leg. O. Mehl, 2 ex. HNHM. – Moluccan Islands, Seram, 12 km SE Wahai, Solea, 16.X.–4.XI.1998, leg. S. Bílý, 1 ex. ZSM. – Papua New Guinea, Torecella Mts., 1700 ft., IV.1939, leg. G. P. Moore, 1 ex. BMNH. – Papua New Guinea, Kiunga, 23.VII.–2.VIII.1969, leg. J. Balogh, 7 ex. HNHM, 1 ex. SMNS. – West Papua, 120 km S Nabire, Unipo-Ebore, 500 m, 4.I.1996, leg. A. Weigel, 1 ex. NME. – West Papua, Japen Island, Kontiunai, 600–700 m, 23.XII.2000, leg. A. Riedel, 6 ex. SMNS. – West Papua, Manokwari, Gunung Meja, 200 m, 30.XII.2000, leg. A. Riedel, 4 ex. SMNS. – West Papua, Japen Island, 20 km E Serui, 2.–5.I.1999, leg. A. Weigel, 1 ex. NME. – Solomon Islands, Guadalcanal Island, 22.IV.1963, leg. P. Greenslade, 1 ex. BMNH.

Remarks: Figured by Schawaller (2004b). Probably, *Platydema townesi* Kulzer, 1957, described from the Caroline Islands, is a junior synonym of this widespread and variable species.

Distribution: Widespread in SE Asia, Japan, Taiwan, Philippines, New Guinea (new record), Moluccan Islands (new record), Solomon Islands (new record).

Platydema rectum Kaszab, 1982

New material: Moluccan Islands, Seram, Sepa, 35 km S Masohi, 15.X.1998, leg. O. Mehl, 1 ex. HNHM. – Moluccan Islands, Seram, Unit O, 35 km E Pasahari, 24.–30.X.1998, leg. O. Mehl, 1 ex. HNHM.

Remarks: Illustrated in Schawaller (2004b). In contrast to the studied paratype, both newly collected specimens from Seram possess only a discal spot and not a humeral spot on the elytra, all other characters coincide. This difference in the colour pattern is considered as infraspecific variation.

Distribution: Tiworo Island (SE Sulawesi), Moluccan Islands (new record).

Platydema simbangense Kaszab, 1939
(Figs. 14, 56–58)

Studied type material: Papua New Guinea, Simbang, Huon Golf, 1898, leg. J. Biró, ♂ holotype (by monotypy) HNHM.

New material: Papua New Guinea, "Simpsonhafen" (= Rabaul), V.1909, leg. H. Schoede, 2 ex. HNHM. – Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, 1899, leg. L. Biró, 1 ex. HNHM. – Papua New Guinea, Prov. Morobe, S Garaina, 700–1700 m, 21.–22.III.1998, leg. A. Riedel, 1 ex. SMNS. – West Papua, Manokwari, Gunung Meja, 200 m, 24.VIII.1991, leg. A. Riedel, 1 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 300 m, 19.–21.IX.1990, leg. A. Riedel, 26 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 300 m, 9.–11.VIII.1991, leg. A. Riedel, 1 ex. SMNS. – West Papua, Jayapura, Sentani, Cyclops Mts., 400–800 m, 7.VIII.1992, leg. A. Riedel, 1 ex. SMNS. – West Papua, Iba, 1300 m, 7.–8.IV.1993, leg. A. Riedel, 1 ex. SMNS. – West Papua, Testega, 1200 m, 31.III.–12.IV.1993, leg. A. Riedel, 1 ex. SMNS. – West Papua, Anggi, Tetaho, Kosmena, 1400–1750 m, 26.–28.III.1993, leg. A. Riedel, 2 ex. SMNS. – Solomon Islands, Guadalcanal Island, Kukum, 2.II.1963, leg. P. Greenslade, 1 ex. BMNH. – Solomon Islands, Guadalcanal Island, Mt. Austen, 19.IX.1962, leg. P. Greenslade, 1 ex. BMNH, 1 ex. SMNS.

Remarks: The specimens show an extraordinary range of the body length from 4.3 mm (holotype) up to 6.0 mm.

Distribution: New Guinea (type locality Simbang), Solomon Islands (new record).

Platydema striolatum Kaszab, 1939
(Figs. 19, 71–73)

Platydema gebieni Kaszab, 1939 **n. syn.**

Studied type material: Papua New Guinea, "Stephansort", Astrolabe Bay, 1900, leg. L. Biró, ♂ holotype (by monotypy) of *striolatum* HNHM. – Same data, ♂ "type" of *gebieni* HNHM, designated herewith as lectotype. – Same data, ♀ "type" of *gebieni* HNHM, now paralectotype.

New material: West Papua, Manokwari, Gunung Meja, 300 m, 22.–23.IX.1990, leg. A. Riedel, 1 ex. HNHM. – West Papua, Manokwari, Gunung Meja, 200 m, 30.XII.2000, leg. A. Riedel, 6 ex. SMNS. – W Papua, Prov. Manokwari, 6 km N Manokwari, Desa Pami, 160 m, 9.III.2007, leg. A. Skale, 2 ex. CRGT.

Synonymy: The armature of the male head (the length of the horns and the extent of setation at the apical part) is somewhat variable (as in other species of *Platydema*, independent from the body length): in the ♂ holotype of *Platydema striolatum* the horns are shorter and the setation at the apical part is indistinct, in the ♂ lectotype of *P. gebieni* the right horn is longer and the setation distinct. All other characters coincide, thus both types from the same locality represent only a single species, for which the valid name *Platydema striolatum* Kaszab, 1939 is herewith selected (according to Art. 24.2 ICZN, the fixation of the precedence is up to the first reviser and page priority is not required).

Distribution: New Guinea (type locality "Stephansort").

Platydema subfascium Walker, 1858

New material: Moluccan Islands, Ambon, 16.II.1961, leg. A. M. R. Wegner, 1 ex. HNHM (*subfascium* det. Kaszab). – Moluccan Islands, Ambon, Laithatu, Soya, 500 m, 8.XI.1998, leg. O. Mehl, 1 ex. HNHM. – Moluccan Islands, Seram, 12 km SE Wahai, Solea, 31.X.–4.XI.1998, leg. J. Horák, 2 ex. ZSM. – West Papua, Batanta Island, Waywesar, 12.–15.I.2004, leg. A. Skale, 1 ex. CASH, 1 ex. CRGT.

Remarks: Figured by Schawaller (2003). Eventually, *Platydema aries* Pascoe, 1869 from Australia might be a synonym of this widespread species.

Distribution: Widespread in SE Asia, Japan, Taiwan, Philippines, Moluccan Islands (new record), New Guinea (new record).

Platydema tricuspis Motschulsky, 1873

New material: Timor, Dilli, 2500 ft., leg. Doherty, 1 ex. BMNH. – Moluccan Islands, Seram, Unit O, 35 km E Pashari, 24.–30.X.1998, collector not labelled, 1 ex. CRGT. – West Papua, Yapen Island, E Serui, 31.VII.1996, leg. N. Ohbayashi, 3 ex. CKAO. – West Papua, Masuni, Manokwari, 11.VIII.1996, leg. N. Ohbayashi, 40 ex. CKAO. – West Papua, 120 km S Nabire, N Unipo, 400 m, 7.I.1996, leg. A. Weigel, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Salawati Island, Kaliam, 21.–24.I.2004, leg. A. Skale, 2 ex. CRGT. – West Papua, Prov. Raja Ampat, Salawati Island, Kaliam, 22.I.2004, leg. A. Weigel, 2 ex. NME. – West Papua, Prov. Raja Ampat, Batanta Island, Wallebet, 18.–21.I.2004, leg. A. Skale, 1 ex. CRGT. – West Papua, Prov. Raja Ampat, Batanta Island, 12 km W Wallebet, 20.I.2004, leg. A. Weigel, 1 ♀ CRGT. – Papua New Guinea, Prov. Morobe, Kaiapit, XII.1978, leg. W. G. Ullrich, 1 ex. ZSM.

Remarks: Illustrated in Schawaller (2004b).

Distribution: Widespread in SE Asia, Philippines, Timor, New Guinea (Gebien 1922 under synonym *Platydema reflexum* Chevrolat, 1878), Moluccan Islands (new record), Australia.

Platydema waterhousei Gebien, 1925

New material: Moluccan Islands, Seram, 35 km E Pasahari, 24.–30.X.1998, leg. O. Mehl, 1 ex. HNHM. – Moluccan Islands, Seram, 35 km E Pasahari, 24.–30.X.1998, leg. J. Horák, 4 ex. CRGT, 2 ex. SMNS. – Moluccan Islands, Seram, 35 km E Pasahari, 24.–30.X.1998, leg. S. Bílý, 1 ex. CRGT.

Variability: The series from the same locality listed above consists of eight specimens, six of them show an aberrant dark pronotum, two possess the "normal" lighter red pronotum. The light colour pattern of the elytra and also the shape of the aedeagus are identical. This colour variability is as yet unknown among several identified specimens of this widespread species. Such a variability might cause some taxonomical problems, see the remarks under *Platydema halmahericum* n. sp. (which could be only a dark insular form/subspecies on Halmahera and New Guinea).

Remarks: Illustrated in Schawaller (2004b).

Distribution: Widespread in SE Asia, Philippines, Moluccan Islands (new record).

3 Descriptions of new Papuan and Moluccan species of *Platydema*

Platydema bacanicum **n. sp.**
(Figs. 10, 45–47)

Holotype (♂): Moluccan Islands, Bacan Island, Labuha, hotel "Buana Lipu", 12.I.2006, leg. A. Skale, CRGT.

Paratype: Moluccan Islands, Bacan Island, valley 3 km S Labuha, 40 m, 13.I.2006, leg. A. Skale, 1 ex. SMNS.

Etymology: Named after the island Bacan, where the type series was collected.

Description: Body length 4.3–4.5 mm. Dorsal side glabrous and with colour pattern, without metallic shine; head dark ferrugineous; pronotum reddish with dark ferrugineous parts along basal and distal margins; elytra dark ferrugineous, in the anterior third with a light transverse band interrupted at the suture, before apices each elytron with a round light spot; tibiae and tarsi lighter (Fig. 10). Head with regular fine punctation. Head in males (Fig. 45): frons medially with a feeble tubercle. Proportions of the antennal segments as in Fig. 46, antennomere

3 short. Pronotum convex, with distinctly finer and sparser punctation than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin not excavated and anterior corners not protruding. Propleura with feeble longitudinal wrinkles, and with short setation. Elytra convex and oval, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 33 punctures). Intervals flat and with nearly invisible punctation, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface feebly wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 47.

Diagnosis: The insular *Platydema bacanicum* n. sp. shows similarities to the widespread *Platydema waterhousei* Gebien, 1925 (figured by Schawaller 2004b) concerning body shape and size as well as colour pattern. In *P. waterhousei*, however, the male head is without armature, the frons between the eyes is narrower, the pronotum is narrower (extremely broad in *P. bacanicum* n. sp.) and bears a denser punctation, and the aedeagus is different. *P. ribbei* Gebien, 1925 from Sulawesi is also similar, and its aedeagus is nearly identical, however in *P. ribbei* the pronotum is also narrow and bears a denser punctation than in *P. waterhousei*, but the male head has a long medial horn.

Platydema cyclopsicum **n. sp.**
(Figs. 11, 48–49)

Holotype (♂): West Papua, Jayapura, Sentani, Cyclops Mts., 400–800 m, 7.VIII.1992, leg. A. Riedel, SMNS.

Etymology: Named after the Cyclops Mountains, where the holotype was collected.

Description: Body length 4.2 mm. Dorsal side glabrous and with unicoloured blue metallic shine; tibiae and tarsi light (Fig. 11). Head with extremely fine, nearly invisible punctation. Head in males (Fig. 48): frons with two symmetrical long horns, apical parts without setation; clypeus medially without tooth. Proportions of the antennal segments unknown, both antennae missing in the holotype. Pronotum slightly convex, with fine punctation slightly larger than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin feebly excavated and anterior corners not protruding. Propleura with feeble longitudinal wrinkles, and with short setation. Elytra only feebly convex and oval, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 40 punctures). Intervals flat and with similar fine punctation as on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 49.

Diagnosis: To be recognized by its small body size with unicoloured metallic shine, the male head with two long symmetrical horns without setation, the relatively flat elytra, and the shape of the aedeagus. Most of the other small unicoloured metallic species from New Guinea and adjacent islands are more convex and have the male head either with asymmetrical horns with different setation, or without armature. *Platydema kaiense* n. sp. and *P. seramicum* n. sp. possess also two symmetrical horns on the male head (short in *P. kaiense* n. sp., long in *P. seramicum* n. sp.), but their bodies are more convex, the elytra have convex intervals and either distinct (*P. kaiense* n. sp.) or feeble (*P. seramicum* n. sp.) striae, and the aedeagi are different (Figs. 49, 52, 55).

Platydema djuremnaicum **n. sp.**
(Figs. 23, 83–85)

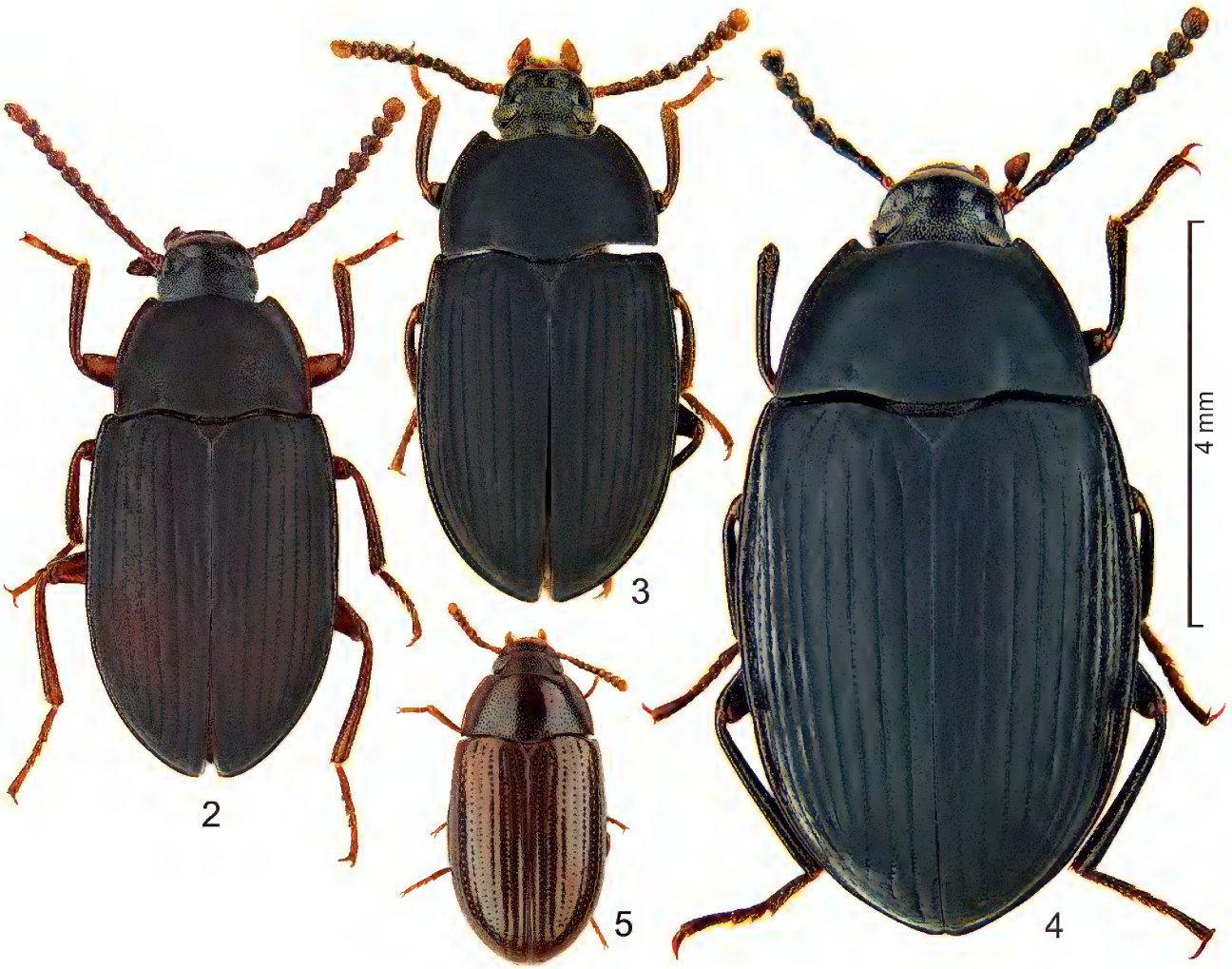
Holotype (♂): West Papua, Prov. Jayawijaya, Djuremna, 1900–2100 m, 9.–11.IX.1992, leg. A. Riedel, SMNS.

Paratypes: Same data as the holotype, 4 ex. SMNS, 1 ex. HNHM. – Papua New Guinea, Prov. Eastern Highlands, Kainatu, Onerunka, 21.VIII.1979, leg. W. G. Ullrich, 1 ex. ZSM.

Etymology: Named after the village Djuremna, in whose vicinity the type series was collected.

Description: Body length 6.5–7.0 mm. Dorsal side glabrous and with colour pattern: head, pronotum and elytra black with distinct green metallic shine; elytra with light transverse humeral spots; tibiae and tarsi somewhat lighter (Fig. 23). Head with extremely fine, nearly invisible punctation. Head in males (Fig. 83): frons with two asymmetrical horns, right horn longer and pointing more upwards, left horn shorter and pointing forwards, apical part of the right horn with distinct setation; clypeus medially with a distinct tooth. Proportions of the antennal segments as in Fig. 84, antennomere 3 short. Pronotum slightly convex, with fine punctation, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin distinctly excavated and anterior corners protruding. Propleura with larger punctation than on pronotum, and with short setation. Elytra convex and oval, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 40 punctures). Intervals flat and with similar fine punctation as on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 85.

Diagnosis: To be recognized by its large body size, a colour pattern with green-metallic dorsal shine and



Figs. 2–5. Dorsal view of *Platydema* male spp. – **2**. *P. fuligineum*, non-type SMNS. **3**. *P. pseudofuligineum* n. sp., holotype SMNS. **4**. *P. papuanum* n. sp., holotype SMNS. **5**. *P. confusum*, non-type SMNS.

light humeral spots on the elytra, the armed male head with asymmetrical shape and setation of the horns, and the shape of the aedeagus. A similar combination of characters does not occur in any other known species of the Oriental and Papuan Regions.

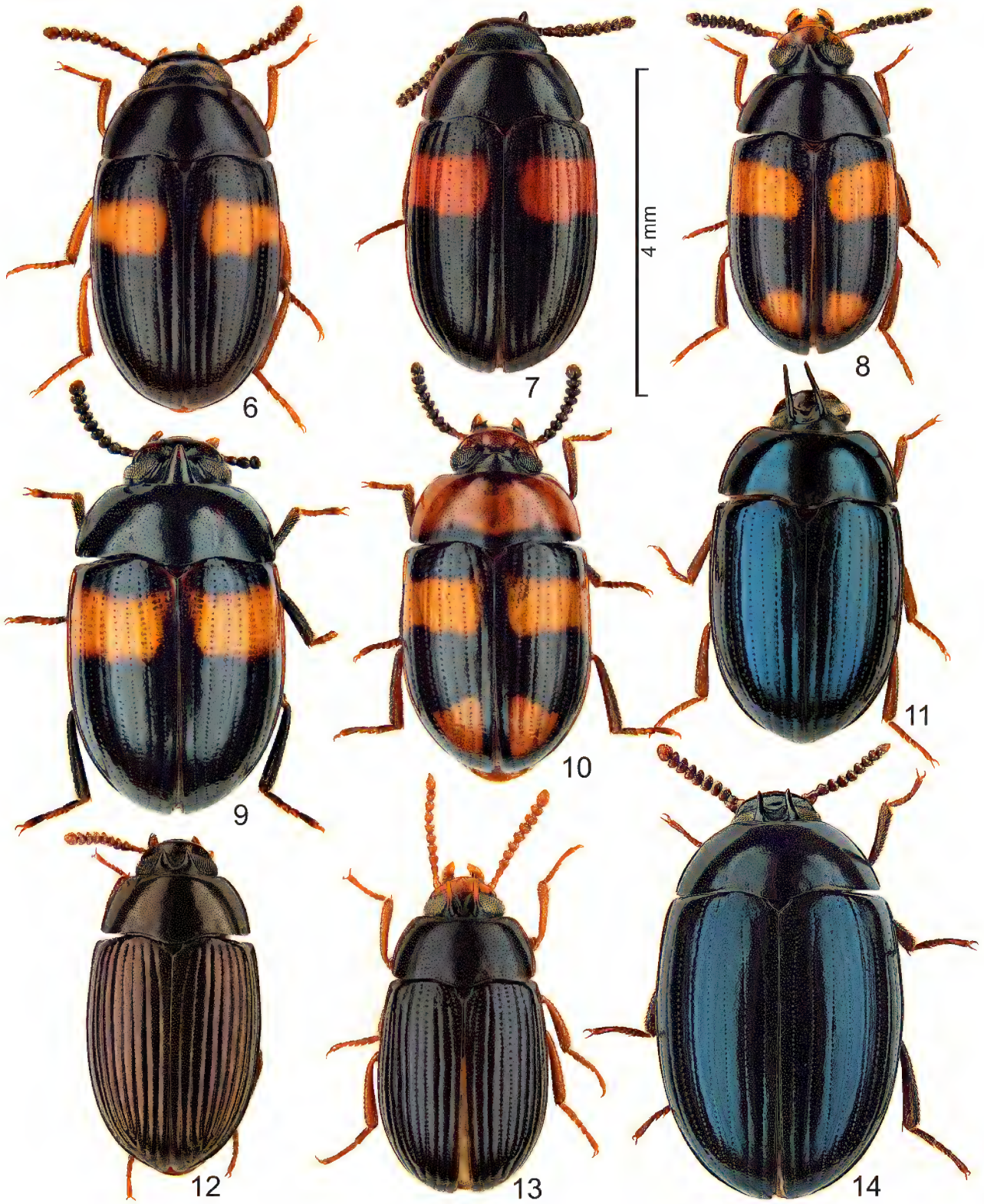
Platydema halmahericum **n. sp.**
(Figs. 6, 36–38)

Holotype (♂): Moluccan Islands, Halmahera, Buli, Maba, 50–650 m, 8.XI.1999, leg. A. Riedel, SMNS.

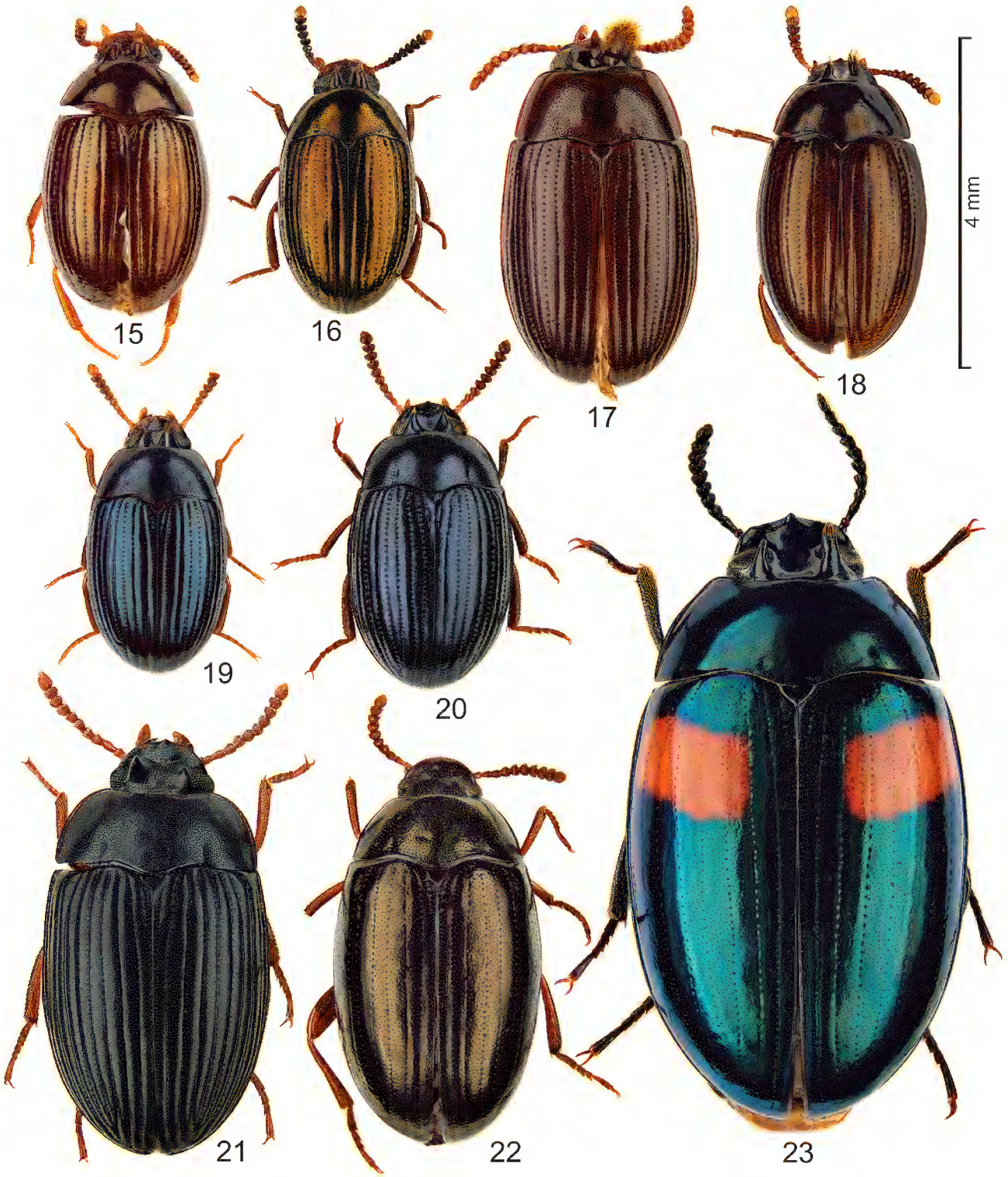
Paratypes: Same data as the holotype, 11 ex. SMNS, 2 ex. CRGT, 2 ex. HNHM. – Papua New Guinea, Kiunga, 23.VII.–2.VIII.1969, leg. J. Balogh, 8 ex. HNHM, 2 ex. SMNS. – West Papua, Prov. Raja Ampat, Waigeo Island, Lopintol, 11.I.2004, leg. A. Skale, 3 ex. CRGT, 1 ex. SMNS.

Etymology: Named after the island Halmahera, where a part of the type series was collected.

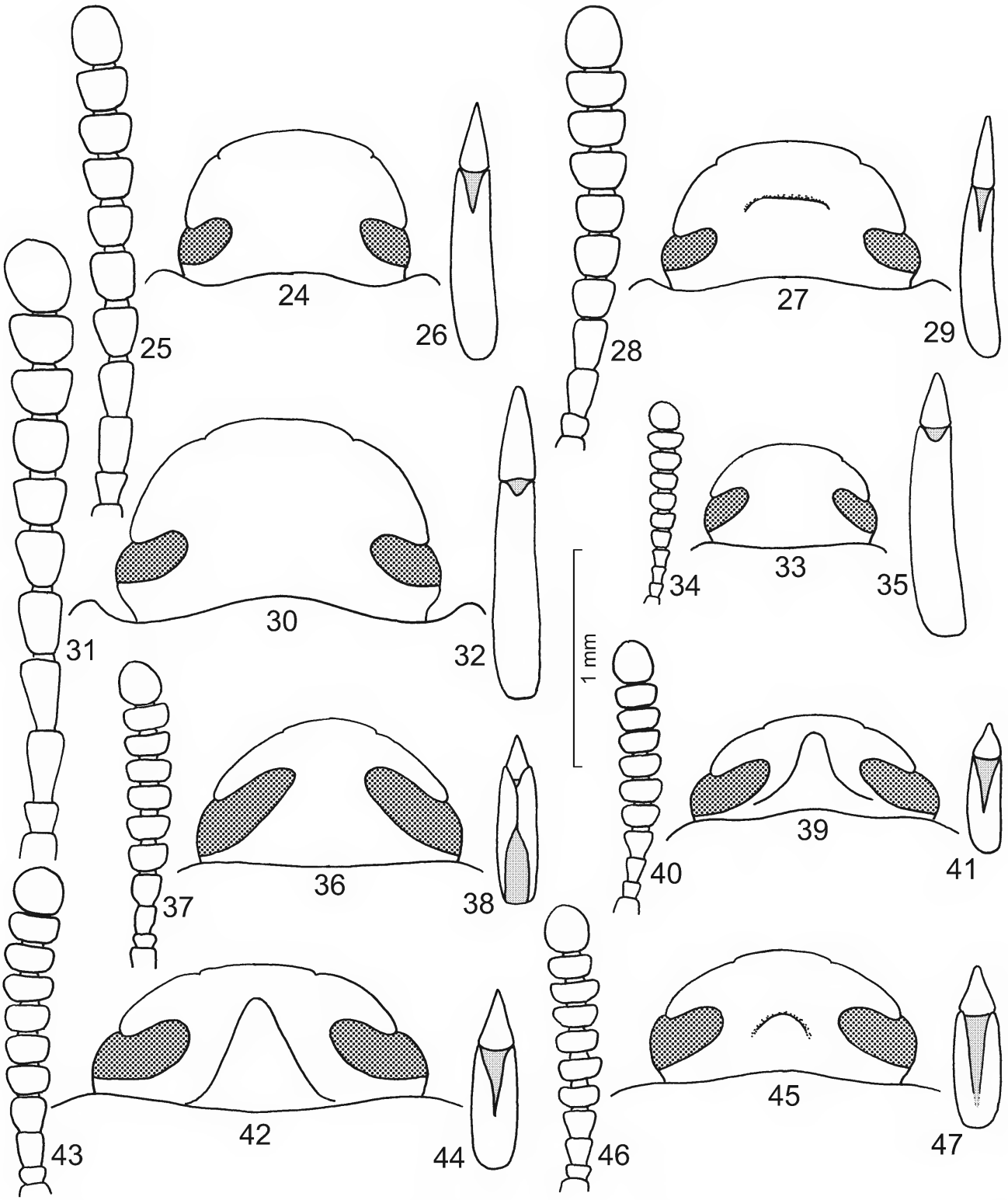
Description: Body length 4.0–4.8 mm. Dorsal side glabrous and with colour pattern: head, pronotum and elytra dark ferrugineous without metallic shine; elytra in the anterior third with a light transverse band interrupted at the suture; tibiae and tarsi light (Fig. 6). Head with regular fine punctation. Head in males (Fig. 36) without sexual characters. Proportions of the antennal segments as in Fig. 37, antennomere 3 short. Pronotum slightly convex, with finer punctation than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin only feebly excavated and anterior corners not protruding. Propleura with larger punctation than on pronotum, and with short setation. Elytra convex and oval, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 40 punctures). Intervals flat or slightly convex



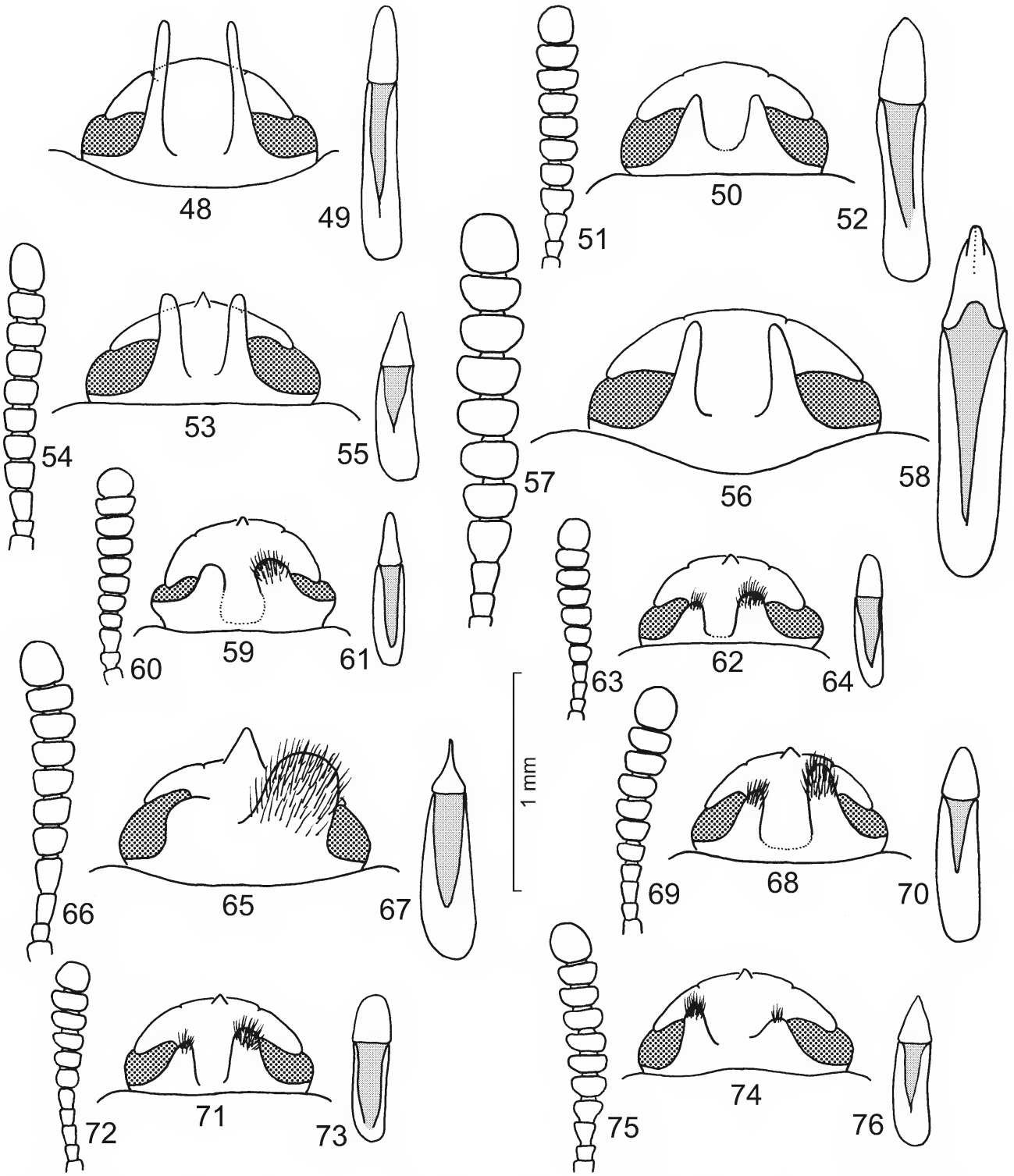
Figs. 6–14. Dorsal view of *Platydema* male (6, 8–14) and female (7) spp. – **6**. *P. halmahericum* n. sp., holotype SMNS. **7**. *P. furcaticorne*, non-type HNHM. **8**. *P. novaeguineense*, non-type SMNS. **9**. *P. skalei* n. sp., holotype CRGT. **10**. *P. bacanicum* n. sp., holotype CRGT. **11**. *P. cyclopsicum* n. sp., holotype SMNS. **12**. *P. kaiense* n. sp., holotype HNHM. **13**. *P. seramicum* n. sp., holotype CRGT. **14**. *P. simbangense*, non-type SMNS.



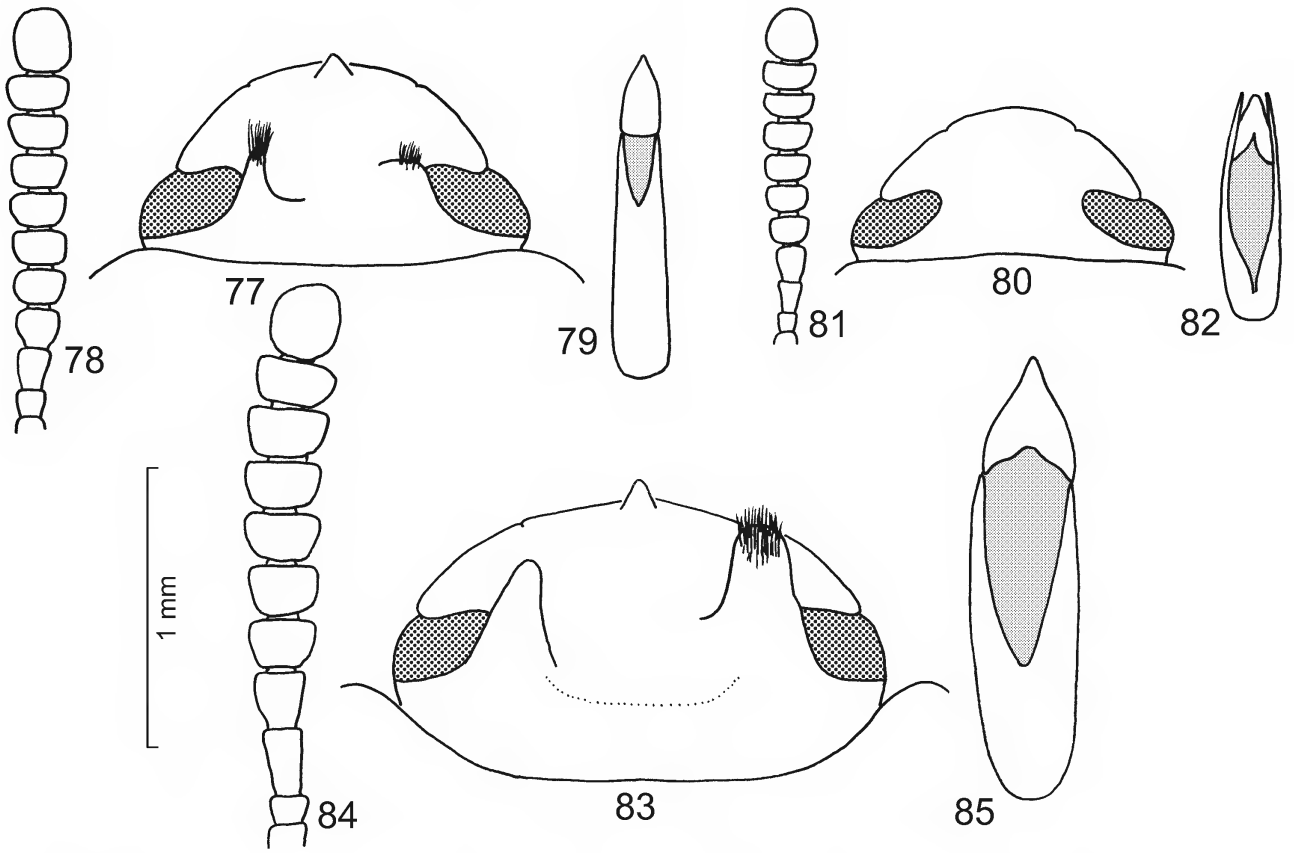
Figs. 15–23. Dorsal view of *Platydema* male spp. – **15**. *P. globigerum*, lectotype HNHM. **16**. *P. denticapitis*, non-type SMNS. **17**. *P. biroi*, lectotype HNHM. **18**. *P. hastatum*, lectotype HNHM. **19**. *P. striolatum*, non-type SMNS. **20**. *P. weigeli* n. sp., holotype SMNS. **21**. *P. asymmetricum*, non-type SMNS. **22**. *P. wamenaicum* n. sp., holotype SMNS. **23**. *P. djuremnaicum* n. sp., holotype SMNS.



Figs. 24–47. Male head, antenna and aedeagus of *Platydema* spp. – **24–26**. *P. fuligineum*, non-type SMNS. **27–29**. *P. pseudofuligineum* n. sp., holotype SMNS. **30–32**. *P. papuanum* n. sp., holotype SMNS. **33–35**. *P. confusum*, non-type SMNS. **36–38**. *P. halmahericum* n. sp., holotype SMNS. **39–41**. *P. novaeguineense*, non-type SMNS. **42–44**. *P. skalei* n. sp., holotype CRGT. **45–47**. *P. bacanicum* n. sp., holotype CRGT.



Figs. 48–76. Male head, antenna and aedeagus of *Platydema* spp. – **48–49**. *P. cyclopsicum* n. sp., holotype SMNS (both antennae missing). **50–52**. *P. kaiense* n. sp., holotype HNHM. **53–55**. *P. seramicum* n. sp., holotype CRGT. **56–58**. *P. simbangense*, non-type SMNS. **59–61**. *P. globigerum*, lectotype HNHM. **62–64**. *P. denticapitis*, non-type SMNS. **65–67**. *P. biroi*, lectotype HNHM. **68–70**. *P. hastatum*, lectotype HNHM. **71–73**. *P. striolatum*, non-type SMNS. **74–76**. *P. weigeli* n. sp., holotype SMNS.



Figs. 77–85. Male head, antenna and aedeagus of *Platydema* spp. – **77–79**. *P. asymmetricum*, non-type SMNS. **80–82**. *P. wamenaicum* n. sp., holotype SMNS. **83–85**. *P. djuremnaicum* n. sp., holotype SMNS.

and with finer and sparser punctation than on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 38.

Diagnosis: *Platydema halmahericum* n. sp. shares with the Oriental widespread *P. planum* Gebien, 1914 the general body size, the unarmed male head and a similar dorsal colour pattern. However, *P. planum* possesses a flatter body shape, the elytra besides the anterior transverse band also with additional light spots before the apices, and a different aedeagus. The Oriental *Platydema monoceros* Gebien, 1925 and *P. aurimaculatum* Gravely, 1915 have a similar oval and convex body and also a similar colour pattern as *P. halmahericum* n. sp., but both have an armed male head with a single distinct horn, and a different aedeagus. *P. furcaticorne* Gebien, 1925 from New Guinea, the Aru and Key Islands and *P. sulawesicum* Schawaller, 2004 from Sulawesi have also a similar colour pattern, but the male heads are armed with two distinct horns, and the aedeagi are different too. Concerning the diagnostic characters see also the following chapter.

Variability: Both series from Halmahera and New Guinea differ only by minute characters, considered as infraspecific variations of both insular populations. In the series from Halmahera the elytral light band is slightly narrower and the elytral punctural rows are slightly more impressed, all other characters including the shape of the aedeagus coincide. The four specimens from the island Waigeo are somewhat smaller in average (4.0–4.2 mm) and the elytral intervals are slightly convex (completely flat in the other specimens), the aedeagus is identical.

Remarks: It cannot be fully excluded, that *Platydema halmahericum* n. sp. is only a subspecies or dark form of the widespread *P. waterhousei* Gebien, 1925 (figured by Schawaller 2004b), because the shape of the aedeagus of both species is identical. It is not impossible that the pale-coloured *P. waterhousei* is widespread in southeastern Asia including the Philippines, and shows no distinct variation of the colour pattern in that large area, but is missing exactly on Halmahera and New Guinea. Furthermore it seems possible, that (as yet only) on the Moluccan island Seram, *P. waterhousei* occurs with the "normal" pale elytral colour pattern, but either with "normal" pale but also with aberrant dark ferrugineous prono-

tum. Probably, we face here an early stage of ongoing insular speciation, which cannot be understood by morphological characters alone. All four specimens from the small island Waigeo possess a dark pronotum. At the present state of taxonomic knowledge I avoid establishing a subspecies and consider the dark populations as a valid species, being different from *P. waterhousei*.

Platydema kaiense **n. sp.**
(Figs. 12, 50–52)

Holotype (♂): Moluccan Islands, Kai Islands (labelled as "Ins.-Key" without further details), HNHM.

Etymology: Named after the Kai (= Key) Islands, where the holotype was collected.

Description: Body length 4.0 mm. Dorsal side glabrous and with unicoloured violet metallic shine; tibiae, tarsi and antenna light (Fig. 12). Head with fine punctation. Head in males (Fig. 50): frons with two symmetrical short horns, apical parts without setation; clypeus medially without tooth. Proportions of the antennal segments as in Fig. 51, antennomere 3 short. Pronotum convex, with similar punctation as on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin feebly excavated and anterior corners not protruding. Propleura with feeble longitudinal wrinkles, and with short setation. Elytra convex and oval, 1.6 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures in distinct striae (third row with about 50 punctures). Intervals convex and with similar fine punctation as on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 52.

Diagnosis: *Platydema kaiense* n. sp. is similar to the widespread *P. marseuli* Lewis, 1894 (figured by Schawaller 2004b) sharing the small unicoloured metallic and convex body, the armature of the male head with two symmetrical horns, and the distinct elytral striae. Both can be separated mainly by a distinctly different shape of the aedeagus (parameres broad pentagonal in *P. kaiense* n. sp., triangular finger-like in *P. marseuli*). See also under *Platydema cyclopsicum* n. sp. and *P. seramicum* n. sp.

Platydema papuanum **n. sp.**
(Figs. 4, 30–32)

Holotype (♂): West Papua, Paniai, Mulia, Wuyuneeri, 1900–2200 m, 6.–7.VII.1994, leg. A. Riedel, SMNS.

Paratypes: West Papua, Prov. Jayawijaya, Borme, 1500–2000 m, 13.–17.VIII.1992, leg. A. Riedel, 7 ex. SMNS, 2 ex. HNHM. – West Papua, Prov. Raja Ampat, Batanta Island, Wallebet, 18.–21.I.2004, leg. A. Skale, 4 ex. CRGT. – West Papua, Prov. Manokwari, 18 km NW Ransiki, Anggi Gida, Kampung Itkau, 1890 m, 4.III.2007, leg. A. Skale, 2 ex. CASH. – West Papua, Prov. Manokwari, Mokwam (Siyoubrig), 1400–1800 m, 24.–28.II.2007, leg. A. Skale, 1 ex. CASH. – West Papua, Prov. Manokwari, Snalmboy (Warmare), 24.II.2007, leg. A. Skale, 1 ex. CKAO. – Papua New Guinea, Prov. Morobe, Aseki, Oiwa, 11.IV.1998, leg. A. Riedel, 3 ex. CRGT. – Papua New Guinea, Prov. Morobe, Kaiapit, XII.1978, leg. W. G. Ullrich, 3 ex. ZSM. – Papua New Guinea, Prov. Morobe, Kaiapit, 30.IX.1979, leg. W. G. Ullrich, 1 ex. ZSM. – Papua New Guinea, Prov. Eastern Highlands, Kainatu, Onerunka, 22.IV.–21.X.1979, leg. W. G. Ullrich, 8 ex. ZSM. – Papua New Guinea, Prov. Eastern Highlands, Kainatu, Onerunka, VII.1981, leg. W. G. Ullrich, 2 ex. ZSM.

Etymology: Named after the Papua tribes, settling on New Guinea.

Description: Body length 6.0–9.0 mm. Dorsal side glabrous and unicoloured black, without metallic shine, surface dull; tibiae, tarsi and antenna somewhat lighter (Fig. 4). Head with regular and fine punctation. Head in males (Fig. 30) without sexual characters. Proportions of the antennal segments as in Fig. 31, antennomere 3 long. Pronotum flat and conical, without punctation, with distinct basal foveae. Basal margin medially unbordered, distal and lateral margins finely and completely bordered; anterior margin distinctly excavated and anterior corners protruding. Propleura smooth as pronotal disc. Elytra flat and of oval shape, 1.6 times as long as wide, besides scutellar row and lateral margin with 8 rows of fine nearly indistinct punctures in distinct striae (third row with about 50 punctures). Intervals feebly convex by the distinct striae, without punctation. Abdominal ventrites with very short setation, laterally with feeble impressions and confluent punctures. Legs without peculiarities, male tarsi not dilated, tibiae rounded and externally without keels. Aedeagus as in Fig. 32.

Diagnosis: *Platydema papuanum* n. sp. shares the large body size with the dull blackish surface, the unmodified male head, and even the similar shape of the aedeagus with the widespread *P. detersum* Walker, 1858 (illustrated by Schawaller 2003). It can be distinguished by the conical shape of the pronotum, flatter elytra with deeply impressed striae, widely separated lateral margins of the elytra, longer antennomeres and unmodified male tibiae. Two other dull blackish species from New Guinea are smaller in average (5.0–6.0 mm), have a broader pronotum with rounder lateral margins, a different aedeagus (*P. pseudofuligineum* n. sp.) or possess even a modified male head (*P. tricuspis*).

Platydema pseudofuligineum **n. sp.**
(Figs. 3, 27–29)

Holotype (♂): West Papua, Wandammen Bay, Wondiwoi Mts., Wasior, 250–600 m, 15.I.2001, leg. A. Riedel, SMNS.

Paratypes: West Papua, Japen Island, Kontiunai, 600–700 m, 23.XII.2000, leg. A. Riedel, 6 ex. SMNS. – West Papua, Testega, 1100–1300 m, 30.III.–2.IV.1993, leg. A. Riedel,

4 ex. SMNS. – West Papua, Testega, Meydoudga, 1100 m, 4.IV.1993, leg. A. Riedel, 1 ex. SMNS. – West Papua, Manokwari, Ransiki, Mayuby, 26.–30.IX.1990, leg. A. Riedel, 2 ex. BMNH. – West Papua, Jayapura, Sentani, Cyclops Mts., 400–800 m, 7.VIII.1992, leg. A. Riedel, 2 ex. SMNS. – West Papua, Fak Fak, 2 km E airstrip, 16.–18.VII.1996, leg. P. Schüle & P. Stüben, 2 ex. SMNS. – Papua New Guinea, Prov. Morobe, "Sattelberg", Huon Golf, leg. L. Biró, 4 ex. HNHM. – Papua New Guinea, Kiunga, 23.VII.–2.VIII.1969, leg. J. Balogh, 2 ex. HNHM, 1 ex. SMNS. – Papua New Guinea, Wau, Kilolo Creek, 26.VIII.1968, leg. I. Loksa, 1 ex. HNHM. – Papua New Guinea, Kokoda, 8.II.1951, leg. J. Sedlacek, 1 ex. HNHM. – West Papua, Prov. Raja Ampat, Salawati Island, 2–4 km N Kalobo, 26.I.2004, leg. A. Skale, 1 ex. CRGT. – West Papua, 120–150 km S Nabire, Unipo-Ebomani, 9.I.1997, leg. A. Weigel, 1 ex. CRGT. – West Papua, Prov. Manokwari, 20 km W Manokwari, Prafi, 160 m, 8.III.2007, leg. A. Weigel, 1 ex. NME.

Etymology: The name refers to the Australian *P. fuligineum* Pascoe, 1869 which looks morphologically similar.

Description: Body length 5.0–6.0 mm. Dorsal side glabrous and unicoloured black, without metallic shine, surface dull; tibiae, tarsi and antenna somewhat lighter (Fig. 3). Head with rough and partly confluent punctation. Head in males (Fig. 27) with a feeble transverse ridge between cheeks. Proportions of the antennal segments as in Fig. 28, antennomere 3 short. Pronotum feebly convex, without punctation, with distinct basal foveae. Basal margin medially unbordered, distal margin finely and lateral margins broadly and completely bordered; anterior margin distinctly excavated and anterior corners protruding. Propleura smooth as pronotal disc. Elytra flat and of oval shape, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of fine nearly indistinct punctures in feeble striae (third row with about 50 punctures). Intervals feebly convex, without punctation. Abdominal ventrites with very short setation, laterally with feeble impressions and confluent punctures. Legs without peculiarities, male tarsi not dilated, tibiae rounded and externally without keels. Aedeagus as in Fig. 29.

Diagnosis: *Platydema pseudofuligineum* n. sp. resembles *P. fuligineum* Pascoe, 1869 from Australia (Figs. 2, 24–26; based on a male from N. S. Wales, 2.X.1908, leg. G. E. Bryant, SMNS [duplicate from BMNH]). Both share the small body size and shape with dull blackish surface. *P. fuligineum* can be distinguished by a distinctly narrower pronotum with a finer lateral margin, a completely unmodified male head, and a different shape of the aedeagus with acute apical part of the parameres. See also under *P. papuanum* n. sp.

Platydema seramicum **n. sp.**
(Figs. 13, 53–55)

Holotype (♂): Moluccan Islands, Seram, Unit O, 35 km E Pasahari, 24.–30.X.1998, leg. J. Horák, CRGT.

Paratype: Moluccan Islands, Seram, 12 km SE Wahai, Solea, 17.I.–6.II.1997, leg. J. Horák, 1 ex. ZSM.

Etymology: Named after the island Seram, where the holotype was collected.

Description: Body length 3.8 mm. Dorsal side glabrous and with feeble unicoloured blue metallic shine; clypeus, legs and antenna light (Fig. 13). Head with fine punctation. Head in males (Fig. 53): frons with two symmetrical long horns, apical parts without setation; clypeus medially with tooth. Proportions of the antennal segments as in Fig. 54, antennomere 3 short. Pronotum slightly convex, with fine punctation similar as on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin feebly excavated and anterior corners not protruding. Propleura with feeble longitudinal wrinkles, and with short setation. Elytra only feebly convex and oval, 1.4 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures with feeble striae (third row with about 35 punctures). Intervals convex and with distinctly finer punctation than on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 55.

Diagnosis: *Platydema seramicum* n. sp. shares the small body size and shape, the unicoloured shining dorsal surface, and the male head with two symmetrical horns with *P. cyclopsicum* n. sp. and *P. kaiense* n. sp. from the investigated area. *P. seramicum* n. sp. can be recognized by an additional tooth on the clypeus (lacking in *P. cyclopsicum* n. sp. and *P. kaiense* n. sp.), distinct convex elytral intervals (flat in *P. cyclopsicum* n. sp., convex in *P. kaiense* n. sp.), and a distinct shape of the aedeagus (Figs. 49, 52, 55). Furthermore, in *P. kaiense* n. sp. the elytra bear distinct striae and the elytral intervals are densely punctured.

Platydema skalei **n. sp.**
(Figs. 9, 42–44)

Holotype (♂): West Papua, Prov. Raja Ampat, Salawati Island, 2–4 km N Kalobo, 26.I.2004, leg. A. Skale, CRGT.

Paratypes: West Papua, Prov. Manokwari, 6 km N Manokwari, Desa Pami, 100 m, 9.III.2007, leg. A. Skale, 1 ex. CASH, 1 ex. CRGT, 1 ex. SMNS.

Etymology: Named in honour of André Skale (Hof/Saale), collector of the type series and other species of Papuan *Platydema*.

Description: Body length 4.5 mm. Dorsal side glabrous and with colour pattern: head, pronotum and elytra dark ferrugineous without metallic shine; elytra in the anterior third with a light transverse band interrupted at the suture; tarsi somewhat lighter (Fig. 9). Head with distinct but not confluent punctation. Head in males (Fig. 42): frons with a medial conical horn with rounded

apical part pointing forwards, apical part without setation; clypeus medially without tooth. Proportions of the antennal segments as in Fig. 43, antennomere 3 short. Pronotum broad and flat, with finer punctation than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin not excavated and anterior corners not protruding. Propleura with larger punctation than on pronotum, and with short setation. Elytra flat and oval, 1.2 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 45 punctures). Intervals flat and with finer punctation than on pronotum, punctation nearly invisible, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 44.

Diagnosis: *Platydema skalei* n. sp. is similar to the Oriental *P. unicornis* Gebien, 1927 (figured by SCHAWALLER 2004b), both share the broad and flat pronotum and elytra, the single medial horn without setation on the male head, and even the aedeagus with similar fused parameres with an acute apical part. However, in *P. skalei* n. sp. the dorsal punctation, particularly on pronotum and the elytral intervals, is distinctly finer and the dorsal surface is more shining, and the elytra bear in the anterior third a broad yellow band (in *P. unicornis* the elytral spots are sinuated). These differences might appear insignificant, but at present state of knowledge I consider both as different species. The other species of *Platydema* on New Guinea with a single medial horn (*P. novaeguineense* Gebien, 1922 and *P. rectum* Kaszab, 1982) are smaller in average, the pronotum and elytra are much more convex, the dorsal colour pattern is different, and the aedeagi are different.

Platydema wamenaicum **n. sp.**
(Figs. 22, 80–82)

Holotype (♂): West Papua, Prov. Jayawijaya, Wamena, Pronggoli, 2000–2400 m, 17.–19.IX.1991, leg. A. RIEDEL, SMNS.

Paratypes: Same data as the holotype, 1 ♀ SMNS. – West Papua, Prov. Paniai, Sinak, 2000–2200 m, 14.–17.XII.1995, leg. A. RIEDEL, 3 ex. ZSM, 1 ex. SMNS.

Etymology: Named after the village Wamena, in whose vicinity the holotype was collected.

Description: Body length 4.5–4.7 mm. Dorsal side glabrous and with unicoloured bronze metallic shine; tibiae, tarsi and antenna light (Fig. 22). Head with distinct but separate punctation. Head in males (Fig. 80) without sexual characters. Proportions of the antennal segments as in Fig. 81, antennomere 3 short. Pronotum slightly convex, with somewhat finer punctation than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin feebly excavated and anterior corners not protruding. Propleura with similar punctation as on pronotum, and with short setation. Elytra convex and oval, 1.6 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 35 punctures). Intervals flat and with distinctly finer and sparser punctation than on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 82.

Diagnosis: *Platydema wamenaicum* n. sp. can be recognized by the small convex body with unicoloured metallic shine and without armature on the male head. This combination is unique among all Papuan species.

Platydema weigeli **n. sp.**
(Figs. 20, 74–76)

Holotype (♂): West Papua, Biak Island, Sepse, 3.X.1990, leg. A. RIEDEL, SMNS.

Paratypes: Same data as the holotype, 2 ex. SMNS. – West Papua, Prov. Raja Ampat, Batanta Island, Waywesar, 13.I.2004, leg. A. WEIGEL, 1 ♂ CRGT. – West Papua, Prov. Raja Ampat, Batanta Island, Waywesar, 12.–15.I.2004, leg. A. SKALE, 1 ♀ CRGT.

Etymology: Named in honour of ANDREAS WEIGEL (Wernburg), one of the collectors of the type series.

Description: Body length 3.5–3.8 mm. Dorsal side glabrous and with unicoloured blue metallic shine; tibiae, tarsi and antenna light (Fig. 20). Head with larger but sparse punctation. Head in males (Fig. 74): frons with two asymmetrical horns, left horn longer and pointing more upwards, right horn shorter and pointing forwards, apical part of the left horn with distinct longer setation, apical part of the right horn with reduced shorter setation; clypeus medially with a distinct tooth. Proportions of the antennal segments as in Fig. 75, antennomere 3 short. Pronotum slightly convex, with somewhat finer punctation than on head, with feeble basal foveae. Basal margin completely unbordered, distal and lateral margins finely and completely bordered; anterior margin feebly excavated and anterior corners not protruding. Propleura with similar punctation as on pronotum, and with short setation. Elytra convex and oval, 1.6 times as long as wide, besides scutellar row and lateral margin with 8 rows of punctures without striae (third row with about 40 punctures). Intervals feebly convex and with similar fine punctation as on pronotum, without setation. Abdominal ventrites with short setation, lateral punctures sometimes confluent and surface wrinkled. Legs without peculiarities, male tarsi not dilated, tibiae externally with crenulated indistinct keels. Aedeagus as in Fig. 76.

D i a g n o s i s : *Platydema weigeli* n. sp. belongs to the small group of small Papuan species with unicoloured metallic surface and with armed head, and is most similar to *P. striolatum* Kaszab, 1939. However, in *P. striolatum* the right horn of the male head is longer and with longer setation (the left horn is longer in *P. weigeli* n. sp.), the pronotum is narrower with conical straight lateral margins (broader with rounded sides in *P. weigeli* n. sp.), the antenna is widened from antennomere 5 on (from antennomere 4 on in *P. weigeli* n. sp.), and the aedeagi are different (Figs. 73, 76).

4 Key to the Papuan and Moluccan species of *Platydema*

This key may be used for the identification of all species of *Platydema* from the investigasted area (Fig. 1). The key is suitable only for males because of the use of sexual characters. Males of several species can be recognized by a modified head, males of species without such modifications can be separated from females only by dissection of the genitalia.

1 Dorsal surface unicoloured dull blackish (Figs. 2–4). **2**
– Dorsal surface shining, either unicoloured dark, with or without metallic shine, or elytra with colour pattern (Figs. 5–14). **5**
2 Male head with two distinct teeth on the frons and with additional medial tooth on the clypeus. – Schawaller 2004b: figs. 7, 187–189. . . . . ***tricuspis***
– Male head without modification or at most with an indistinct medial tubercle. **3**
3 Pronotum broad with rounded lateral margins, male head unmodified; middle and posterior tibiae in males abruptly bent in variable extent. – Schawaller 2003: figs. 25–27; pl. IV, fig. 6. . . . . ***detersum***
– Pronotum longer, either conical or with rounded margins, in the latter case male head with transverse tubercle; all legs without modifications. **4**
4 Pronotum conical, male head without modification, elytra with distinct striae, body length 6.0–9.0 mm. – Figs. 4, 30–32. . . . . ***papuanum* n. sp.**
– Pronotum with rounder lateral margin, male head with transverse tubercle, elytral rows only in feeble striae, body length 5.0–6.0 mm. – Figs. 3, 27–29. . . . . ***pseudofuligineum* n. sp.**
5 Male head without modifications or frons at most with a feeble medial tubercle (Figs. 33, 45, 80). **6**
– Male head with a single medial horn or with a pair of symmetrical or asymmetrical horns, horns with or without setation (Figs. 42, 48, 65). **11**
6 Dorsal side unicoloured (Figs. 5, 22). **7**
– Dorsal side with distinct colour pattern (Figs. 6, 10). **8**
7 Small species (around 3 mm), pronotum with large punctures at the sides but lacking on the disc, elytral rows with large punctures, intervals slightly convex. – Figs. 5, 33–35. . . . . ***confusum***
– Larger species (4.5–4.7 mm), pronotum with regular fine punctation, elytral rows with fine punctures, intervals flat. – Figs. 22, 80–82. . . . . ***wamenaicum* n. sp.**
8 Smaller species (around 3 mm), elytral intervals with microsetation. – Schawaller 2004b: figs. 16, 136–138. . . . . ***pallidicolle***
– Larger species (4.0–4.8 mm), elytral intervals completely glabrous (Figs. 6, 10). **9**
9 Male head with a feeble medial tubercle, pronotum broad. – Figs. 10, 45–47. . . . . ***bacanicum* n. sp.**
– Male head without modification, pronotum narrower (Fig. 36). **10**
10 Elytra in the anterior third with a single light transverse band interrupted at the suture, pronotum dark. – Figs. 6, 36–38. . . . . ***halmahericum* n. sp.**
– Elytra besides the light transverse humeral band in the posterior part with additional light spots, pronotum usually light, but sometimes also dark. – Schawaller 2004b: figs. 17, 190–192. . . . . ***waterhousei***
11 Male head with a single medial horn without setation (Figs. 39, 42). **12**
– Male head with a pair of symmetrical or asymmetrical horns, horns with or without setation (Figs. 48, 65, 74). **14**
12 Dorsal side light castaneous, elytra with 1–2 dark spots. – Schawaller 2004b: figs. 12, 148–150. . . . . ***rectum***
– Dorsal side dark ferrugineous, elytra in the anterior third with a light transverse band and in the posterior part with or without light spot (Figs. 8–9). **13**
13 Larger species (4.5 mm), pronotum broad and flat, elytra flat, elytra in the anterior third with a light transverse band. – Figs. 9, 42–44. . . . . ***skalei* n. sp.**
– Smaller species (3.5–4.0 mm), pronotum and elytra narrower and more convex, elytra in the anterior third with a light transverse band and in the posterior part with an additional light spot. – Figs. 8, 39–41. . . . . ***novaeguineense***
14 Male head with a pair of symmetrical horns without setation (Figs. 48, 53). **15**
– Male head with a pair of asymmetrical horns and at least one horn with setation at the apical part (Figs. 65, 74). **19**
15 Dorsal side dark ferrugineous, elytra in the anterior third with a light transverse band (♀ see Fig. 7; ♂ see Gebien 1925: pl. 1, fig. 9). . . . . ***furcaticorne***
– Dorsal side unicoloured dark, with metallic shine (Figs. 11, 14). **16**
16 Elytra with punctural rows in striae, intervals convex (Figs. 12–13). **17**
– Elytra with punctural rows without striae, intervals flat (Figs. 11, 14). **18**
17 Male head besides the pair of long horns with an additional distinct medial tooth at the clypeus, fused parameres triangular. – Seram Island. Figs. 13, 53–55. . . . ***seramicum* n. sp.**
– Male head without additional tooth at the clypeus, fused parameres pentagonal. – Kai Islands. Figs. 12, 50–52. . . . . ***kaiense* n. sp.**
18 Pronotum broader, pronotum and elytra flat, lateral margins of pronotum and elytra broadly separated, fused parameres tongue-shaped. – Figs. 11, 48–49. . . . . ***cyclopsicum* n. sp.**
– Pronotum narrower, pronotum and elytra more convex, lateral margins of pronotum and elytra finely separated, fused parameres triangular. – Figs. 14, 56–58. . . . . ***simbangense***
19 Left horn of the male head longer and with longer and denser setation at the apical part (Figs. 74, 77). **20**
– Right horn of the male head longer and with longer and denser setation at the apical part (Figs. 65, 83). **21**
20 Larger species (4.5–6.0 mm), pronotum and elytra flat, dorsal surface unicoloured blackish without metallic shine, elytral intervals with microsetation. – Figs. 21, 77–79. . . . . ***asymmetricum***
– Smaller species (3.5–3.8 mm), pronotum and elytra convex, dorsal surface with metallic shine, elytral intervals completely glabrous. – Figs. 20, 74–76. . . . . ***weigeli* n. sp.**
21 Dorsal surface with colour pattern (Fig. 23). **22**
– Dorsal side unicoloured dark (Figs. 15, 17). **23**
22 Larger species (6.5–7.0 mm), elytra with light transverse hu-

meral spots, dorsal side with metallic shine. – Figs. 23, 83–85. . . . . ***djuremnaicum* n. sp.**

– Smaller species (4.0–5.0 mm), elytra with light undulated humeral bands and ill-defined lighter apical area, dorsal side without metallic shine. – SCHAWALLER 2003: figs. 16–18; pl. IV, fig. 4. . . . . ***subfascium***

23 Right horn of the male head extremely developed and with extended long setation, left horn nearly absent, clypeus with strong medial tooth, aedeagus with long and thin acute apical part of the fused parameres. – Figs. 17, 65–67. . . . . ***biroi***

– Right horn of the male head longer than the left but not extremely developed, setation present at the apical part only, clypeus with smaller medial tooth, shape of the aedeagus different (Figs. 61, 70). **24**

24 Body shape globular, eyes narrow, left smaller horn of male head without setation. – Figs. 15, 59–61. . . . . ***globigerum***

– Body shape longer oval, eyes broader, left smaller horn of male head with setation (Figs. 62, 68, 71). **25**

25 Somewhat larger species (3.5–4.5 mm), right horn on male head parallel, setation at the apical part in wider extent, fused parameres of aedeagus triangular with acute apical part. – Figs. 18, 68–70. . . . . ***hastatum***

– Somewhat smaller species (3.0–3.2 mm), right horn on male head conical, setation only at the extreme apical part, fused parameres of aedeagus different (Figs. 64, 73). **26**

26 Elytral intervals feebly convex, fused parameres of aedeagus broader with rounded apical part. – Figs. 19, 71–73. . . . . ***striolatum***

– Elytral intervals flat, fused parameres of aedeagus narrower with rounded apical part. – Figs. 16, 62–64. . . . ***denticapitis***

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Manuscript received: 3.VIII.2007, accepted: 27.IX.2007.

New and poorly known Chrysomelidae (Coleoptera) from the islands of Bali and Lombok (Indonesia)

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Abstract

Six new species and one new subspecies (Coleoptera: Chrysomelidae) from the Indonesian islands of Bali and Lombok are described: *Lema sumbawensis lomboki* **n. ssp.**, *Lema baliana* **n. sp.** (Criocerinae); *Taumacera centromaculata* **n. sp.**, *Paraplotes granulata* **n. sp.** (Galerucinae); *Hespera foveipennis* **n. sp.**, *Hespera lombokana* **n. sp.**, *Nisotra insulana* **n. sp.** (Alticinae). *Lema gestroi* Jacoby, 1884, *Trichochrysea hirta* Fabricius, 1801 and *Orthaltica laticollis* Scherer, 1971 are first recorded from these islands.

Keywords: Chrysomelidae, new species, Bali, Lombok, Indonesia.

Zusammenfassung

Sechs neue Arten und eine neue Unterart (Coleoptera: Chrysomelidae) von den indonesischen Inseln Bali und Lombok werden beschrieben: *Lema sumbawensis lomboki* **n. ssp.**, *Lema baliana* **n. sp.** (Criocerinae); *Taumacera centromaculata* **n. sp.**, *Paraplotes granulata* **n. sp.** (Galerucinae); *Hespera foveipennis* **n. sp.**, *Hespera lombokana* **n. sp.**, *Nisotra insulana* **n. sp.** (Alticinae). *Lema gestroi* Jacoby, 1884, *Trichochrysea hirta* Fabricius, 1801 und *Orthaltica laticollis* Scherer, 1971 werden zum ersten Mal für diese Inseln nachgewiesen.

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1 Introduction

During a recent visit in the Staatliches Museum für Naturkunde in Stuttgart I had the opportunity to study numerous newly collected chrysomelids from the Indonesian islands Bali and Lombok. Chrysomelidae of these islands are very poorly studied and published. Hitherto only a single publication is available about the leaf-beetles of the subfamily Galerucinae from Bali (Mohamedsaid 2001); the chrysomelid beetles of Lombok remained unknown. After a detailed study of the SMNS material, six new species and one new subspecies are recognized and described herein. I take the opportunity and add three new records of chrysomelid species from these islands.

Acronyms of depositories

LM Collection of Dr. Lev Medvedev, Moscow, Russia
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany

Acknowledgements

I thank my friend Dr. Wolfgang Schawaller (SMNS) for the possibility to study this interesting material and for his hospitality during my visits in the State Natural History Museum in Stuttgart.

2 Taxonomy and distribution

2.1 Subfamily Criocerinae

Lema (Petauristes) sumbawensis lomboki **n. ssp.**

Holotype (♂): Indonesia, Lombok, Sesaot, 500 m, 1.II.1994, leg. L. Bolm, SMNS.

Paratype: Indonesia, Lombok, Senaro, N slope of Rinjani, 1100 m, 2.–5.II.1994, leg. L. Bolm, 1 ♀ LM.

Description: Body length 7.0–8.3 mm. Pronotum entirely fulvous; all other characters identical to the nominate subspecies.

Diagnosis: The nominate subspecies *L. sumbawensis* Jacoby, 1895 from Sumbawa possesses a black stripe on the base of pronotum, delimited anteriorly by the prebasal impression; it has a body length of 6.9–7.3 mm.

Lema (Lema) gestroi Jacoby, 1884

Material examined: Indonesia, Bali, Danau Buyan, 1300 m, 19.–21.II.1994, leg. L. Bolm, 2 ex. SMNS.

Remarks: Both specimens from Bali possess an entirely black apical quarter of the elytra, while the nominate *L. gestroi* Jacoby, 1884 usually has a preapical black band. However, this species, which was previously known

from Sumatra, Nias and Java, is rather variable and specimens from Sumatra in my collection (det. HEINZE) also have a black apical quarter of the elytra. *L. delauneyi* Baly, 1889, recorded from Vietnam and Thailand, may represent a junior synonym of this species.

Lema (Lema) baliana **n. sp.**

Holotype (sex not determined): Indonesia, Bali, Danau Buyan, 1300 m, 19.–21.II.1994, leg. L. BOLM, SMNS.

Paratypes: Same data as holotype, 1 ex. LM. – Indonesia, Bali, Ubud, NNE Denpasar Sayan, Yeh Ayung, 21.XI.1993, leg. PANKOW, 2 ex. SMNS.

Description: Upperside metallic blue, with 4–5 basal antennomeres which are reddish at the base or below; legs fulvous with more or less darkened tarsi; abdomen fulvous with black basal sternite. – Head as wide as pronotum, sparsely pubescent; clypeus punctuate, frontal grooves divergent in a right angle; vertex slightly convex, punctuate, with deep longitudinal groove. Antennae reach the middle of the elytra; proportions of antennomeres 10-6-10-11-16-15-14-13-13-12-15; preapical antennomeres about 2.5 times as long as wide. Pronotum 1.1 times as wide as long, constricted just behind the middle; pronotal surface with a transverse impression in the basal third; surface shining, distinctly punctuate. Scutellum triangular, impunctate. Elytra 1.65 times as long as wide, slightly narrowed posteriorly and broadly rounded at apex; elytral surface with a deep postbasal impression and regular rows of deep punctures. Body length 4.4–4.8 mm.

Diagnosis: This species is characterized by its colour pattern, which is not found in any other congener of the Indonesian fauna. *L. nilgiriensis* Jacoby, 1903 from southern India is somewhat similar concerning these characters, but differs in a distinctly punctated head and pronotum.

2.2 Subfamily Eumolpinae

Trichochrysea hirta Fabricius, 1801

Material examined: Indonesia, Lombok, Sembalun Lawang, Mt. Rinjani, 1700 m, 6.–8.II.1994, leg. L. BOLM, 1 ♂ SMNS.

Distribution: Known from Malaysia, Sumatra, Bali, Java, Nias, and Sulawesi; first record from Lombok.

2.3 Subfamily Galerucinae

Taumacera centromaculata **n. sp.** (Figs. 1, 2)

Holotype (♂): Indonesia, Bali, Danau Buyan, 1300 m, 19.–21.II.1994, leg. L. BOLM, SMNS.

Paratypes: Same data as holotype, 1 ♂ LM, 1 ♀ SMNS.

Description (♂): Fulvous, antennal segment 3 dorsally black, next antennomeres more or less darkened; pronotum with a central piceous spot confluent with a narrow stripe at anterior margin; scutellum, underside of body, tibiae and tarsi black. – Head impunctate; frontal tubercles subquadrate with acute and elongate anterior angles, bordered posteriorly by a transverse impression. Clypeus long, with longitudinal ridge. Antennae reach the apical third of elytra; proportions of antennomeres 10-2-14-7-7-8-7-7-7-8-9; segment 3 strongly thickened, about twice as long as wide, with a deep oval groove at the upper surface (Fig. 1); preapical antennomeres about 4–5 times as long as wide. Pronotum 1.35 times as wide as long, broadest in the anterior third, lateral sides slightly rounded; surface microsculptured, impunctate except a few punctures in the prebasal transverse depression. Scutellum triangular, impunctate. Elytra 1.65 times as long as wide, with a feeble basal convexity and a postbasal impression, elytral surface finely punctuate and microsculptured. Segment 1 of male anterior tarsi not widened. Aedeagus (Fig. 2) thin and long, with acute apex. Body length 6.0–6.4 mm. — (♀): Colour pattern identical, but antennal segment 3 entirely fulvous. Third antennomere simple. Body length 7.2 mm.

Diagnosis: This species belongs to the *Taumacera deusta* species-group (as defined by REID 1999) and is similar to *T. laevipennis* Jacoby, 1886 and *T. midtibialis* Mohamedsaid, 1998, but can be distinguished by a different dorsal colour pattern, a different shape of the male antennomere 3, and simple mid tibiae. MOHAMEDSAID (2001) mentioned some unnamed species of *Taumacera* Thunberg, 1814 from Bali, the new species possibly being one of them.

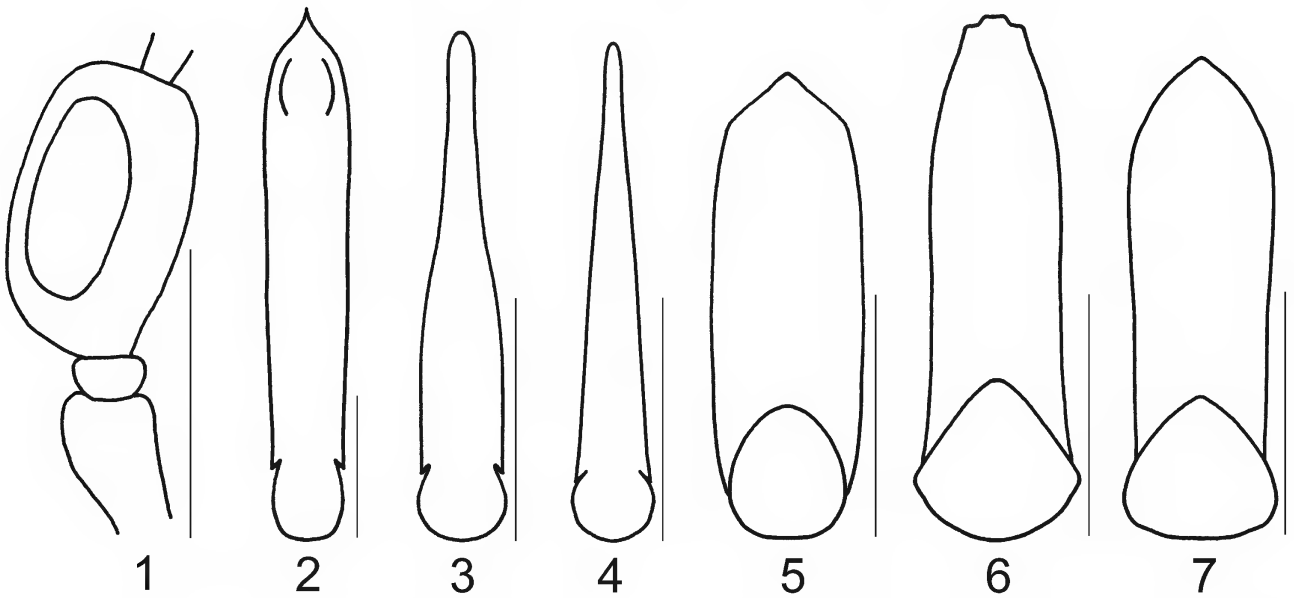
Paraplotes granulata **n. sp.**

Holotype (♀): Indonesia, Lombok, Sapit–Sembalun Bumbung, 900–1500 m, 14.–16.II.1994, leg. L. BOLM, SMNS.

Paratypes: Same data as holotype, 3 ♀♀ SMNS, 1 ♀ LM.

Description: Fulvous, antennae black with segments 1 and 2 fulvous, 10 and 11 pale flavous, but apex of segment 11 black; elytra black with a feeble bronze sheen; ventral side of body castaneous to piceous. – Head impunctate; frontal tubercles elongate triangular, with acute apices, bordered posteriorly by a sharp impressed line. Antennae reach the apical third of the elytra; proportions of antennomeres 10-2-10-8-7-7-7-8-9-8-10; preapical antennomeres about 3–4 times as long as wide. Pronotum twice as wide as long, slightly divergent anteriorly, lateral margins straight, anterior angles thickened and acute; surface shining and impunctate. Elytra 1.5 times as long as wide, broadened posteriorly; surface dull and coarsely granulate, with short dark pubescence, lateral margins sharp; epipleura impunctate, longitudinally concave. Body length 4.5–4.7 mm.

Diagnosis: The new species differs from other known species of the genus by its pale flavous apical antennomeres. *P. rugosa* Laboissière, 1933 from Vietnam is



Figs. 1–7. Basal antennomeres 1–3 (1) and aedeagi (2–7) of Indonesian Chrysomelidae. – **1–2**. *Taumacera centromaculata* n. sp. **3**. *Hespera foveipennis* n. sp. **4**. *H. lombokana* n. sp. **5**. *Nisotra insulana* n. sp. **6**. *N. gemella*. **7**. *N. chrysomeloides*. – Scale: 0.5 mm.

relatively similar, but *P. granulata* n. sp. is distinguished by its fulvous labrum and by its coarsely granulate elytra with metallic surface. The other known species of *Paraplotes* are described from continental Asia, except one species from Taiwan.

2.4 Subfamily Alticinae

Hespera foveipennis **n. sp.** (Fig. 3)

Holotype (♂): Indonesia, Lombok, Sembalun Lawang, Mt. Rinjani, 1700 m, 6.–8.II.1994, leg. L. Bolm, SMNS.

Paratypes: Same data as holotype, 7 ex. SMNS, 2 ex. LM.

Description: Black or piceous, elytra sometimes castaneous; labrum, antennae and legs fulvous, apical antennomeres and posterior femora darkened; pubescence of head and dorsal side of body golden, rather short. – Body elongate, slightly widened posteriorly. Head densely punctuate and microsculptured on vertex; frontal tubercles triangular, convex and microsculptured. Antennae reach the apical quarter of the elytra; proportions of antennomeres 10-5-10-12-15-13-12-11-11-10-11; preapical antennomeres about 2.5–3 times as long as wide. Pronotum 1.2 times as wide as long, lateral sides slightly rounded; pronotal surface finely and densely punctuate. Elytra 1.6 times as long as wide; elytral surface finely and densely punctuate, with very narrow interspaces; each elytron with a deep and broad impression near the middle of the lateral margin, delimited externally by a distinct fold. Last visible abdominal sternite with a deep impression. Segment 1 of male anterior tarsus feebly widened. Aedeagus (Fig. 3) cuneiform with very long and thin apical process, straight in lateral view. Body length 2.5–2.8 mm.

Diagnosis: This species is similar to *H. philippinica* L. Medvedev, 1993 from the Philippines, but differs in its distinct impression on the elytra and in its very long apical process of the aedeagus.

Hespera lombokana **n. sp.** (Fig. 4)

Holotype (♂): Indonesia, Lombok, Sapit–Sembalun Bumbung, 900–1500 m, 14.–16.II.1994, leg. L. Bolm, SMNS.

Description: Black; three basal segments of the antennae, anterior and mid legs dark fulvous; pubescence of dorsal side white. – Body elongate, parallel-sided. Head densely punctuate, pubescent and microsculptured on vertex; frontal tubercles triangular, convex, microsculptured. Antennae reach the apical third of the elytra; proportions of antennomeres 10-3-7-12-12-12-12-11-10-10-12; preapical antennomeres about 4 times as long as wide. Pronotum 1.4 times as wide as long, lateral sides very slightly rounded; pronotal surface finely and densely punctuate, with short pubescence. Elytra 1.65 times as long as wide; elytral surface without any depressions, finely and extremely densely punctuate, interspaces very narrow and not larger than punctures, surface microsculptured, and covered with short hairs which are mostly directed backwards. Last visible abdominal sternite medially with a smooth groove. Segment 1 of male anterior tarsi not widened. Aedeagus (Fig. 4) cuneiform, straight in lateral view. Body length 3.3 mm.

Diagnosis: This new species is similar to *H. nigra* Chen, 1934 from Borneo, but can be distinguished by the colour pattern and by the shape of the aedeagus.

Orthaltica laticollis Scherer, 1971

Material examined: Indonesia, Lombok, Sembalun Lawang, Mt. Rinjani, 1700 m, 6.–8.II.1994, leg. L. Bolm, 9 ex. SMNS, 2 ex. LM. – Indonesia, Lombok, Sapit–Sembalun Bumbung, 900–1500 m, 14.–16.II.1994, leg. L. Bolm, 8 ex. SMNS. – Indonesia, Bali, Danau Buyan, 1300 m, 19.–21.II.1994, leg. L. Bolm, 1 ex. SMNS.

Distribution: Originally described from Singapore. New records from Bali and Lombok.

Nisotra insulana **n. sp.** (Fig. 5)

Holotype (♂): Indonesia, Bali, Danau Buyan, 1300 m, 19.–21.II.1994, leg. L. Bolm, SMNS.

Paratypes: Same data as holotype, 19 ex. SMNS, 1 ex. LM. – Indonesia, E Lombok, Sapit, SE slope of Mt. Rinjani, 14.–16.II.1994, leg. L. Bolm, 4 ex. SMNS, 2 ex. LM.

Description: Red fulvous; six apical antennomeres and ventral side of body black, only apical abdominal sternite reddish, elytra metallic bluish green. – Body ovate. Clypeus punctuate, vertex punctuate at the sides, broadly impunctate in the middle. Antennae reach the anterior third of the elytra; proportions of antennomeres 4-3-3-3-3-4-4-4-4-4-6; preapical antennomeres about 2.2 times as long as wide. Pronotum 1.7 times as wide as long, with rounded lateral margins; surface finely and sparsely punctuate; anterior margin with a deep, sharp and long groove on each side (about $^2/_5$ of pronotum length) and with a shallower and short groove on each side of the base. Elytra 1.2 times as long as wide, with feeble humeral tubercles, densely and confusedly punctuate without rows, interspaces of punctures shining. Segment 1 of male anterior and mid tarsi moderately widened. Aedeagus as in Fig. 5. Body length 3.8–4.2 mm.

Diagnosis: Six species of this genus are as yet known from Indonesia (Kimoto 2001). *Nisotra rotundata* Jacoby, 1896 from Sumatra has a fulvous dorsal side. Both *N. chapuisi* Baly, 1876 from Java and *N. terminata* Jacoby, 1894 possess a reddish elytral apex. *N. javana* Motschulsky, 1866 from Java is a synonym of *N. gemella* Erichson, 1834 (Medvedev 2006). *N. gemella* Erichson, 1834 and *N. chrysomeloides* Jacoby, 1885, which are widely distributed in the Oriental region including Indonesia, are very similar to *N. insulana* n. sp., but can be distinguished by their irregular rows of punctures on the elytra and by different shapes of the aedeagi (Figs. 6, 7).

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Manuscript received: 18.IV.2007, accepted: 21.V.2007.

The identity of *Myxexoristops arctica* (Zetterstedt), with notes on some other *Myxexoristops* (Diptera: Tachinidae)

Christer Bergström

Abstract

Tachina arctica Zetterstedt, 1838 is removed from synonymy with *Myxexoristops blondeli* (Robineau-Desvoidy, 1830) and established as a valid species of *Myxexoristops* Townsend, 1911. A full description is provided for this species. *Tachina porcula* Zetterstedt, 1859 is treated as nomen dubium, and *Tachina petiolinervis* Zetterstedt, 1859 is established as nomen oblitum; both are removed from synonymy with *Myxexoristops blondeli*. A key to the north European species of *Myxexoristops* is presented.

Keywords: Tachinidae, *Myxexoristops*, new synonymy, key, Scandinavia.

Zusammenfassung

Tachina arctica Zetterstedt, 1838 wird als gültige Art von *Myxexoristops* Townsend, 1911 aufgefasst, und nicht wie bisher als ein Synonym von *Myxexoristops blondeli* (Robineau-Desvoidy, 1830). Eine vollständige Beschreibung von *Tachina arctica* wird gegeben. *Tachina porcula* Zetterstedt, 1859 wird als nomen dubium verstanden und *Tachina petiolinervis* Zetterstedt, 1859 als nomen oblitum; beide sind nicht mehr Synonyme von *Myxexoristops blondeli*. Die Arbeit beinhaltet einen Bestimmungsschlüssel für die nordeuropäischen *Myxexoristops*-Arten.

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1 Introduction

The genus *Myxexoristops* Villeneuve, 1911 constitutes a morphologically and biologically homogeneous group within the large and multiform tribe Goniini (Herting 1984, O'Hara & Wood 2004). This tribe is defined by microtype eggs which are deposited in numbers on the food-plants of the hosts and which are subsequently ingested by the victims (compare Herting 1960). All *Myxexoristops* species are, so far as known, parasitoids of sawfly larvae (Hymenoptera: Symphyta).

At least all Scandinavian *Myxexoristops* share the following features: Eyes densely haired. Fronto-orbital plate with 2–3 reclinate inner orbital setae (posteriormost seta smaller), females in addition with 2–3 proclinate outer orbital setae. Ocellar setae moderately strong, proclinate. Parafacial narrowing below, at narrowest point narrower than width of first flagellomere. Facial ridge with setae and additional setulose hairs which are not reaching the upper half. Parafacial bare or at most with some minute hairs directly below the lowest frontal seta. Subcranial cavity 0.60–0.75 times as long as the length of frons. Prosternum haired. Proepisternum bare, except for 1–2 seta(e) and some hairs at lower margin. Postpronotum with 4–5 (rarely 6) setae, the 3 basal setae arranged in an obtuse triangle, and 1–2 smaller setae anterior to the basal setae. Katepisternum with 3 (rarely 4) setae. Katepimeron bare or with 1–4 minute hairs restricted to anterior fourth. First postsutural supra-alar seta longer and stouter than notopleural setae. Scutellum with 4 pairs of setae, the lateral setae 0.6–1.0 times as long as the basal setae. Wing with second costal section normally bare ventrally, but with small black hairs in one species (*M. stolida*). Mid tibia usually with only 1 anterodorsal seta, but in *M. bonsdorffi* with 2–3 setae. Syntergite 1+2 with mid-dorsal depression extending back to hind margin. Tergite 2 with a pair of median marginal setae.

Myxexoristops is externally very similar to *Phebellia* Robineau-Desvoidy, 1846, but is well separated from this genus by its different eggs and oviposition behaviour.

The genus *Myxexoristops* (sensu Herting 1964) is widely distributed in the Palaearctic and Nearctic regions. Up to the present seven species of *Myxexoristops* have been recorded from the Palaearctic region (Herting & Dely-Draskovits 1993), six of them are known from Europe (Tschorsnig et al. 2004), and one (*M. grandicornis* Mesnil, 1955) only from Japan. Two species occur in the Nearctic region (O'Hara & Wood 2004).

In this paper the current concept of *Myxexoristops arctica* (Zetterstedt, 1838) is revised and its synonymy

with *Myxexoristops blondeli* (Robineau-Desvoidy, 1830) is shown to be based on a misidentification. Furthermore, information on types and synonymy is given for some other species of *Myxexoristops*.

Acknowledgements

This paper was prepared within the Swedish Taxonomy Initiative, by contract with ArtDatabanken (The Swedish Species Information Centre) – SLU (Swedish University of Agriculture Sciences), Uppsala. I am grateful to Stig Andersen (Copenhagen), Jim O'Hara (Ottawa), Hans-Peter Tschorsnig (Stuttgart) and Joachim Ziegler (Berlin) for critically reading the manuscript, and to Göran Liljeberg (Västerljung), Malin Birgersson and Mattias Sundström (both Uppsala) for their technical support preparing the images for this paper. Sincere thanks are due to the following colleagues, who enabled me to study material kept in their institutions or private collections: Stig Andersen (Copenhagen), Roy Danielsson (Lund), Roger Engelmark (Umeå), Juha Laiho (Helsinki), Jim O'Hara (Ottawa), Thomas Pape (Copenhagen), Knut Rognes (Madla), Hans-Peter Tschorsnig (Stuttgart), Nigel Wyatt (London), and Joachim Ziegler (Berlin).

2 Materials and Methods

This study was based on the examination of the following material representing six Palaearctic and two Nearctic species of *Myxexoristops*:

M. arctica (Zetterstedt, 1838): 7 specimens (+ holotype) from Norway and Sweden (see material listing in chapter 3);
M. abietis Herting, 1964: 26 specimens from Denmark [SA], Sweden [SA, CB, MZLU], Finland [MZH], and Russia [MZH];
M. bicolor (Villeneuve, 1908): 3 specimens from Poland and Sweden [CB];
M. blondeli (Robineau-Desvoidy, 1830): 1 ♂ from Denmark (Sjælland, Rude Skov, 23.VI.1984, S. Andersen [SA]; dissected), and 13 specimens from Germany [SMNS, ZMHB], Switzerland [SMNS] and Britain [BMNH];
M. bonsdorffi (Zetterstedt, 1859): 25 specimens from Sweden [CB, RE, NHRS, MZLU], Finland [MZH] and Russia [MZH];
M. fronto (Coquillett, 1897): 4 specimens from Canada [CNC];
M. neurotomae (Sellers, 1943): 8 specimens from Canada [CNC];
M. stolida (Stein, 1924): 140 specimens from Denmark [SA, NHM], Norway [KR], Sweden [CB, MZLU, NHRS], Finland [MZH], Russia [MZH] and Germany [ZMHB].

The dissection of the male terminalia (three dissections each of *M. arctica* and *M. blondeli*) was performed following the methods described by Andersen (1996) and O'Hara (2002). For the preparation of the images genital parts and a wing were mounted on microscopic slides in polyvinyllactophenol, sometimes with an admixture of chlorazol black E.

External morphological images (Figs. 1–2) were taken with a Nikon D2X digital camera mounted to a bellow and a macro-optical tube. Images of terminalia (Figs. 3–11) were taken with a digital camera mounted on a stereoscopic microscope. To create a completely focused image, a series of images of each object were taken at different focal planes. Using HeliconFocus, a program that combines the focused areas from the several partially focused images, creates one completely focused image.

Data on the labels of type material are listed using the following symbols: / = end of a line; // = end of a label (from top to bottom on the same pin).

The dissected male terminalia are preserved in glycerol in a small plastic tube pinned together with the specimen.

Terminology of external morphology and terminalia as well as measurements and ratios of head follow Tschorsnig (1985) and Tschorsnig & Richter (1998).

Acronyms of depositories

BMNH The Natural History Museum (formerly British Museum Natural History), London, UK (N. Wyatt)
CB Private collection of C. Bergström, Uppsala, Sweden
CNC Canadian National Collection, Biosystematics Research Centre, Ottawa, Canada (J. E. O'Hara)
KR Private collection of K. Rognes, Madla, Norway
MZH Zoological Museum Helsinki, Finland (J. Laiho).
MZLU Museum of Zoology, Lund University, Sweden (R. Danielsson)
NHM The Natural History Museum, University of Copenhagen, Denmark (T. Pape)
NHRS Swedish Museum of Natural History (= Naturhistoriska Riksmuseet), Department of Entomology, Stockholm, Sweden (B. Viklund)
RE Private collection of R. Engelmark, Umeå, Sweden
SA Private collection of S. Andersen, Copenhagen, Denmark
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany (H.-P. Tschorsnig)
ZMHB Museum für Naturkunde, Humbolt-Universität, Berlin, Germany (J. Ziegler)

3 *Myxexoristops arctica* (Zetterstedt, 1838)

Material

Holotype (♂) from **Norway**, Finnmark, with the following labels: "*T. arctica* / ♂ Bossek (handwritten Zetterstedt label) // [1981 / 521] // *Myxexoristops* / *blondeli* R. D. ♂ / B. Herting det. // Holotype ♂ / *Tachina* / *arctica* Zett. 1838 / det. Bergström 2003" [MZLU, Diptera Scandinaviae collection, drawer 22].

Additional specimens: **Norway**: 1 ♂, Telemark (TEi), EIS 16, Fyresdal, Aslestad-Slystøl, 650 m, 7.VII.1980, K. Rognes leg. [KR] (dissected). — **Sweden**: 1 ♂, Hälsingland, Bergsjö, Bodsjön, 31.VII.1993, RN 68727/15620, C. Bergström leg. [CB] (dissected). – 1 ♂, Lp. in. / And (= Lapponia in. / Andersson leg.) [NHRS] (dissected). – 1 ♀, Lule lappmark, Jokkmokk, Vajmat, Keutajape SO lake Kåikaure, 10.VII.2006, RN 73842/16649, C. Bergström leg. [CB]. – 1 ♀, Uppland, Uppsala, Nåsten (Forsbacka), 18.VIII.1996, RN 66362/15973, C. Bergström leg. [CB]. – 1 ♀, Västerbotten, Umeå, Gubböle, 17.VII.1997, Roger Engelmark leg. [RE]. – 1 ♀, Jämtland, Alsen, Berge, 8.VIII.1840, J. W. Zetterstedt leg. [MZLU] (see also *Tachina diligens*).

History of the use of the name *Tachina arctica*

In August 7, 1821, during his first journey to Scandinavian "Lappland", J. W. Zetterstedt climbed mount Skaaddavaara between Altengaard and Bossekop in Finnmark Fylke, Norway. On this particular day he collected a single tachinid specimen in the subalpine zone close to the mountain peak. Several years later he described this specimen under the name *Tachina arctica* (Zetterstedt 1838: 645). In the original description he wrote: "Hab. in Finmarkia occidentali rarissime; in monte subalpino Skaaddavaara,

non longe a capite septentr. distante, d. 7. Aug. semel inveni. (Lapponia.)". This description was slightly changed by ZETTERSTEDT (1844: 1187): "Hab. in Finmarkia occidentali Norvegiæ rarissime; in monte subalpino Skaaddavaara, non longe a Nord-Cap distante 7 Aug. 1821 inveni.". The holotype is mounted on a very strong pin that precludes a study of the postsutural area of the scutum. Both wings possess prominent tears; left fore and mid legs as well as tarsal segments on right fore and mid legs are missing.

There has been much confusion in the past concerning the correct use of the name *Tachina arctica* Zetterstedt. RINGDAHL (1934: 267), apparently the first reviser, stated that the type present in the Diptera Scandinaviae collection most likely represented an *Exorista* species ("*Exorista* sp. dub."). He also noted that the specimen would key out as *Exorista pexops* (Brauer & Bergenstamm, 1891) using the key of STEIN (1924) [*M. pexops*, the type-species of *Myxexoristops* Townsend, is today regarded as a junior synonym of *M. blondeli*]. However, RINGDAHL (l. c.) also stated that the description of STEIN is somewhat deviant and therefore considered that there was only a very small possibility that *arctica* was identical with *pexops*. He later (1945: 27) changed his opinion – without explanation – and regarded *T. arctica* as a synonym of *Eumea mitis* (Meigen, 1824). MESNIL (1955: 446) – without having seen the type – relied on RINGDAHL's first opinion and listed *arctica* as a synonym of *M. blondeli*, a concept which however also included *Myxexoristops stolida* (Stein). HERTING (1964) established *M. blondeli* (Robineau-Desvoidy, 1830) and *M. stolida* (Stein, 1924) as two valid species; he studied the type of *M. arctica*, but nevertheless maintained this species in synonymy with *M. blondeli*.

Identity: *Tachina arctica* herein revised is removed from synonymy with *Myxexoristops blondeli* (Robineau-Desvoidy, 1830) and established as the name of a valid species in the combination *Myxexoristops arctica* (Zetterstedt, 1838).

Description of the species

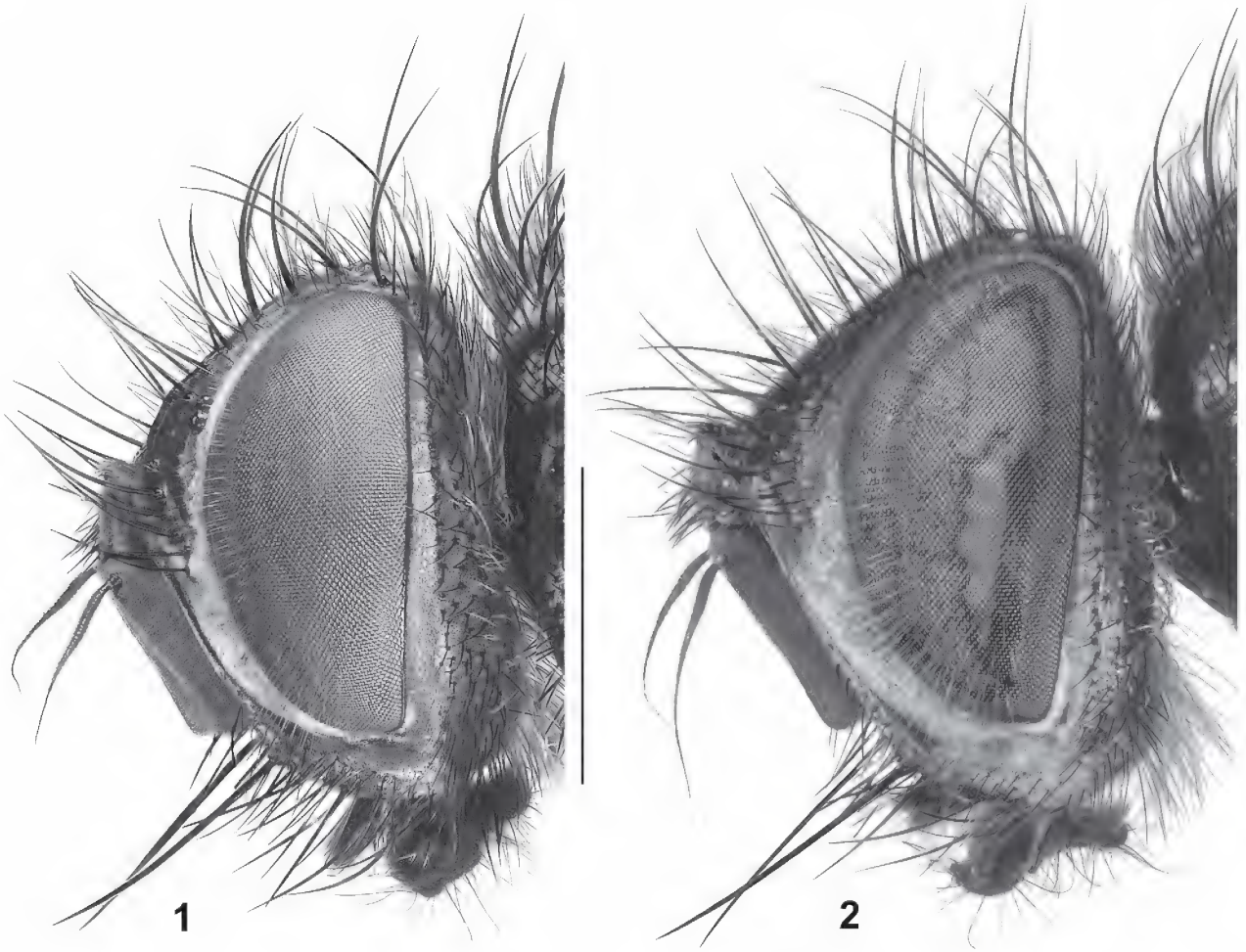
Male (statements within square brackets refer to holotype):

Colour and pruinosity: Head mainly black with a greyish white pruinosity; frontal vitta reddish brown to brown; face at mouth margin, anterior portion of parafacial, and genal groove reddish brown or brownish. Antenna black; arista black or brownish black. Palpus entirely black. Thorax black, dorsally covered with thin greyish white pruinosity; with 5 (less distinct) dark longitudinal stripes; middle stripe absent in front of suture. Black lateral thoracic stripe in front of suture somewhat indistinct, ending wedge-shaped at level of the posteriormost inner post-humeral seta; black lateral thoracic stripe behind the suture, insignificantly narrowing, extending backwards to the level of the posteriormost dorsocentral seta (most distinctly so in females). Tegula and basicosta black. Calypter yellowish white with fringe more yellow. Halter with base and stem brownish yellow, knob brownish. Legs black or – in older specimens – brownish black. Syntergite 1+2 without pruinosity. Tergites 3–4 dorsally with basal bands of greyish white pruinosity covering anterior $^2/_3$–$^3/_4$, towards hind margins replaced by a more brownish pruinosity; interrupted in the middle by an unbroken black longitudinal stripe. Tergite 5 dorsally with a greyish white basal band covering anterior $^2/_5$–$^1/_2$ (slightly more laterally) of that segment.

Head (Fig. 1): Eyes densely covered with long white hairs. Frons about as long as or slightly longer than face; in lateral view only slightly projecting, at level of antennal insertion about 0.4 times as wide as small diameter of eye; dorsally at its narrowest point 0.63–0.79 [0.70] times as wide as an eye in dorsal view. Interfrontal area at midpoint approximately as wide as the width of the parafrontal area at that level. Ocellar setae proclinate, usually as strong as or stronger than anteriormost inner reclinate orbital setae; postocellar setae strong. Inner vertical seta 0.6–0.7 [0.70] of eye-height; outer vertical seta 0.5–0.6 [0.63] times as long as inner vertical seta. Row of 10–12 frontal setae descending to about level of base of first flagellomere, or slightly beneath; 2–3 inner reclinate orbital setae. Parafacial with 0–4 [2–3] minute hairs descending below level of lowest frontal seta; strongly narrowing below, at its narrowest point approximately as wide as the maximal width of palpus. Occiput behind postocular row of setae with numerous black setulae, white hairs restricted to central and lower parts of occiput and postgena. First flagellomere relatively short, 2.4–3.1 [2.8] times as long as wide and 3.1–3.8 [3.1] times as long as pedicel. Arista evenly thickened in about basal fourth, and then gradually tapering towards tip. Sclerotized part of prementum about 2 times as long as wide. Palpus widened and slightly flattened apically, about as long as first flagellomere; tip densely covered by black hairs.

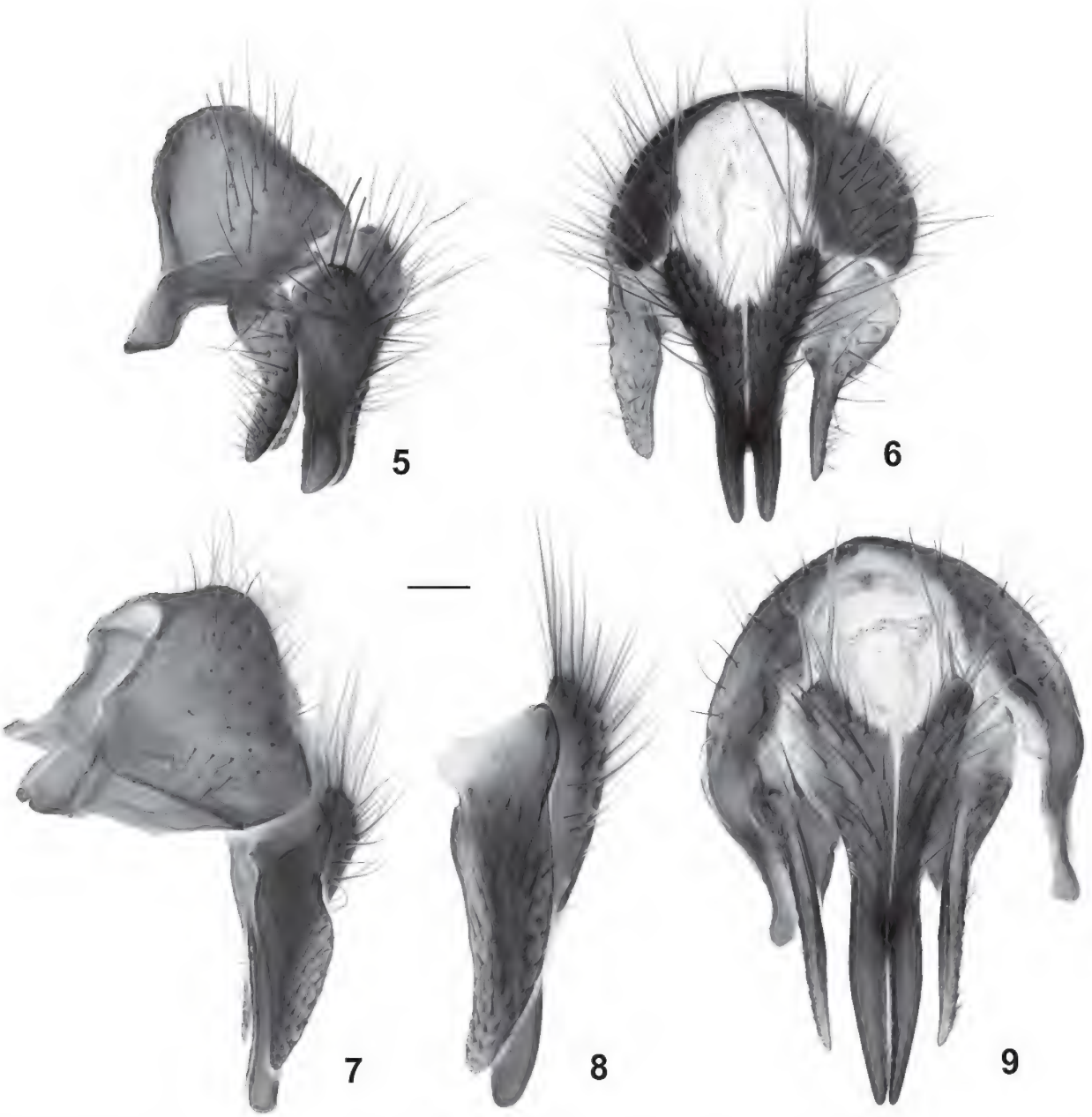
Thorax: Postpronotum with 4–5 setae; 3 basal setae arranged in an obtuse triangle and 1–2 [2] weaker setae in front of the middle and inner basal setae. Scutum with 3+3 pairs of acrostichal setae, 3+4 pairs of dorsocentral setae and 1+3 pairs of intra-alar setae. First postsutural supra-alar seta is stronger than notopleural setae. Katepisternum with 3 setae and numerous long, sometimes setulose hairs. Katepimeron bare. Anepimeral seta weak, distinctly weaker than the lowest katepisternal seta. Scutellum with 4 pairs of setae along margin; basal pair strong, almost as strong as subapical pair; lateral pair 0.6–0.7 times as long as subapical pair; apical pair slightly raised and crossed; dorsal surface of scutellum with a pair of discal setae, subequal to lateral setae.

Wing: Costal spine weakly developed, only slightly stronger than the surrounding costal setulae; second costal section ventrally bare; fourth and fifth costal section to-



Figs. 1–2. *Myxexoristops* spp., ♂ head, lateral views. – **1**. *M. arctica* (Zetterstedt) [Norway, Telemark]. **2**. *M. blondeli* (Robineau-Desvoidy) [Germany, Baden-Württemberg, Kaiserstuhl]. – Scale: 1 mm.

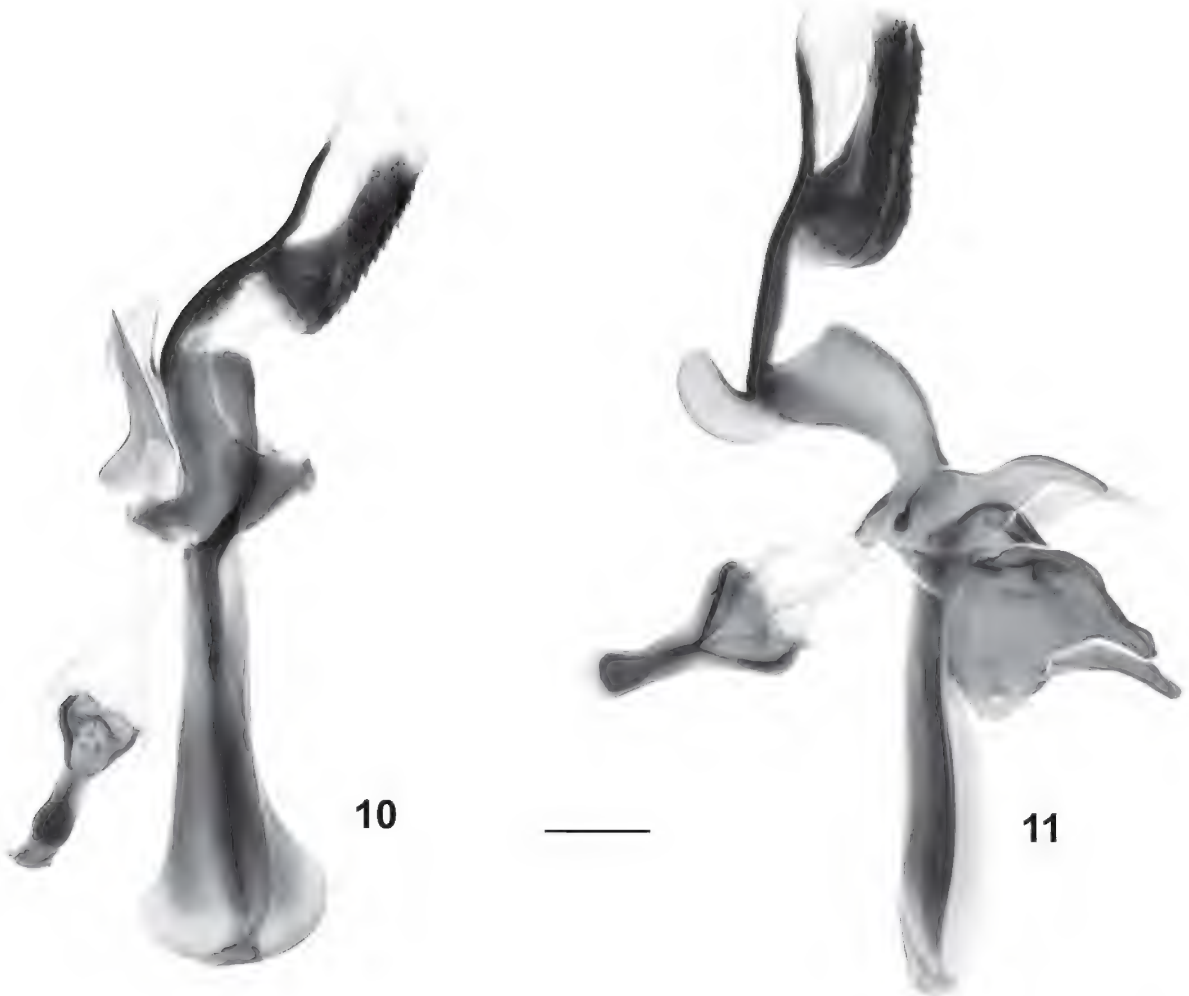
Figs. 3–4. *Myxexoristops* spp., ♂ abdominal sternite 5. – **3**. *M. arctica* (Zetterstedt) [Norway, Telemark]. **4**. *M. blondeli* (Robineau-Desvoidy) [Denmark, Sjælland, Rude Skov]. – Scale: 0.1 mm.



Figs. 5–9. *Myxexoristops* spp., ♂ hypopygium, lateral (5, 7–8) and caudal (6, 9) views. – **5–6**. *M. arctica* (Zetterstedt) [Sweden, Hälsingland (5); Norway, Telemark (6)]. **7–9**. *M. blondeli* (Robineau-Desvoidy) [Germany, Baden-Württemberg (7); Denmark, Sjælland (8); Britain, Wiltshire, Vernditch (9)]. – Scale: 0.1 mm.

gether 3.3–3.9 [3.8] times as long as sixth costal section. Vein R_{4+5} dorsally with 3–4 setulae at base. Bend of vein M obtuse and without an appendage; apical section of vein M distinctly concave. Section of vein M between crossvein dm-cu and bend 1.7–2.1 [1.7] times as long as distance between bend of vein M and margin of wing. Last section of vein CuA_1 distinctly shorter than crossvein dm-cu.

Legs: Claws and pullvilli on fore legs about 1.2 times as long as tarsal segment 5, the latter 1.6–1.7 times as long as tarsal segment 4. Fore tibia with 2 posterior setae and a row of 6–8 short anterodorsal setulae; preapical anterodorsal seta undifferentiated; preapical dorsal seta well developed. Mid tibia with 1 strong anterodorsal seta, 2 posterior setae and 1 strong ventral seta. Hind tibia with an irregular row of 12–16 anterodorsal setae, including a strong seta inserted at middle; moreover with a row of 4–5 short posterodorsal setae including a strong seta at height of strong anterodorsal seta; 2(3) strong anteroventral setae;



Figs. 10–11. *Myxexoristops* spp., ♂ aedeagus, pregonites, postgonites, aedeagal apodeme, and ejaculatory apodeme in lateral views. – **10**. *M. arctica* (Zetterstedt) [(Norway, Telemark]. **11**. *M. blondeli* (Robineau-Desvoidy) [Britain, Wiltshire, Vernditch]. – Scale: 0.1 mm.

2 preapical dorsal setae; preapical posteroventral seta of hind tibia undifferentiated.

Abdomen: Ground-vestiture on tergite 3 half recumbent, distinctly more erect on tergite 4. Tergite 2 with a pair of median and a pair of lateral marginal setae. Tergite 3 with a pair of median and 1–2 pairs of lateral marginal setae; with a pair of median discal setae but without differentiated lateral discal setae. Tergite 4 with a complete row of 8–10 [8] marginal setae; medially with 2(–4) strong discal setae and often some additional setulose hairs, without differentiated lateral discal setae. Tergite 5 with two complete rows of discal setae in addition to the row of marginal setae.

Male terminalia (Figs. 3, 5–6, 10): Sternite 5 approximately 0.8 times as long as wide; with deep U-formed cleft occupying about anterior half; posterior lobe on surface with setae and setulae and along medio-apical margin densely haired. Sternite 6 well developed, strongly asymmetrical. Tergite 6 divided into two hemitergites, without setulae and with spiracle 6 situated in membrane. Segment 7+8 narrow, with some setulae, and with spiracle 7 in that segment. Cerci short, in dorsal view approximately 3.5 times as long as broad at midpoint, apical half almost parallel sided; cerci apically separated from each other by a well defined cleft about as long as $^2/_5$ of basal suture, dorsal margin in lateral view slightly curved and tip evenly curved. Surstylus distinctly shorter than cercus; in lateral view curved anteriorly and distinctly diverging from cercus; gradually narrowing towards apex and densely covered by long setulose hairs. Aedagus: basiphallus with basal projection; membranous epiphallus inserted dorso-apically; distiphallus with ventral plate of distiphallus not much expanded laterally and with lateroventral surface densely covered with spinules.

Body length: 5.2–7.2[7.2] mm (n = 4).

Female (differences from male):

Head: Frons at its narrowest point 0.76–0.86 times as wide as an eye in dorsal view. Parafrontal area with row of 6–10 frontal setae descending to about level of base of first flagellomere or sometimes slightly further; 2 outer proclinate orbital setae and 2 inner reclinate orbital setae (the posteriormost seta often slightly lateroclinate). First flagellomere 2.8–3.2 times as long as pedicel. Fore leg with claws and pullvilli 0.6–0.7 times as long as tarsal segment 5, the latter 1.3–1.4 times as long as tarsal segment 4. Dorsal ground vestiture on tergite 3 mainly recumbent, but erect or suberect between the median marginal and discal setae, and also on lateral edge; tergite 4 predominantly with erect or semi-erect setulae but sometimes with a small area of recumbent setulae close to the anterior margin. Tergite 3 with 2–3 median discal setae; tergite 4 with 2–6 irregular discal setae.

Body length: 7.0–7.4 mm (n = 3).

Distribution

M. arctica is only recorded from Scandinavia. All examined specimens from Norway and Sweden previously assigned to *M. blondeli* are actually specimens of *M. arctica*. The true *M. blondeli* is therefore only represented in the Nordic countries by a single male specimen from Denmark (see chapter 2).

Biology

Habitats are deciduous woodland often close to boggy areas. The female from Keutajape was collected from foliage of an osier (*Salix* sp.) in an open fen area.

Host of *M. arctica* are unknown. It is unlikely that some of the recorded hosts of *M. blondeli* might refer to *M. arctica*, because the breedings were not from Scandinavia: the Pamphiliidae *Neurotoma saltuum* (Linnaeus, 1758) from Germany and United Kingdom (Herting 1964), and the Tenthredinidae *Mesoneura opaca* (Fabricius, 1775) from Germany (Herting 1961) and *Pristiphora moesta* (Zaddach, 1876) probably from Central Europe (the record in Tschorsnig & Herting 1994 is based on a breeding of Zinnert which was not published elsewhere). But it is of course probable that so nearly related species as *M. blondeli* and *M. arctica* might have similar hosts.

Differences from other species of *Myxexoristops*

M. arctica and *M. blondeli* can usually be distinguished from other European species of *Myxexoristops* by their entirely black scutellum (not quite stable in *M. arctica*). Specimens of *M. stolida* sometimes also have an entirely dark scutellum, but are then recognized by the minute black setulae ventrally on the second costal section. *M. arctica* can be separated from *M. blondeli* as shown in the key below.

My examination and also the descriptions of the two Nearctic species *Myxexoristops fronto* (Coquillett) [see Coquillett 1897: 96 and Sellers 1943: 96] and *M. neurotomae* (Sellers) [see Sellers 1943: 85] show that neither of them is conspecific with *M. arctica*. The combination of characters of *M. fronto* and *M. neurotomae* – as shown below – does neither apply to *M. arctica* (see description presented above) nor to any other European *Myxexoristops*.

The study of 2 ♂♂ and 2 ♀♀ of *M. fronto* gives the following results: scutellum mostly black but distinctly reddish brown at tip, sometimes in almost apical third; palpus entirely yellow; frons in male at narrowest point 0.7–0.8 times, in female 0.8–0.9 times as wide as an eye; first flagellomere in male 4.6–5.3 times, in female 3.8–4.0 times as long as pedicel; tibia and ventral part of femur reddish yellow in male, legs yellowish in female; hairs of anterior spiracle yellowish, lid of posterior spiracle yellowish or whitish; second costal section ventrally without black setulae; abdomen in male with distinct reddish yellow spot dorso-laterally on tergite 3 and sometimes also more or less visible on tergite 4, in female ventrally (including tergite 5) and also dorso-laterally extensively yellow. ♀♀: ground vestiture of tergite 3 erect medio-dorsally distinctly recumbent dorso-laterally; on tergite 4 entirely erect dorsally.

My examination of 3 ♂♂ and 3 ♀♀ of *M. neurotomae* shows the following features: scutellum extensively black but mostly narrowly reddish brown at extreme tip; palpus brownish yellow; frons in male at narrowest point 0.7–0.8 times, in female 0.9–1.0 times as wide as an eye; first flagellomere in male 4.7–5.3 times, in female 3.3–3.8 times as long as pedicel; legs uniformly brownish or brownish black; hairs of anterior spiracle and lid of posterior spiracle dark; second costal section ventrally without minute black setulae; abdomen in male mostly black but sometimes with indistinct reddish yellow spot laterally on tergite 3 and sometimes also on tergite 4, in female ventrally (except for tergite 5) predominately reddish yellow and dorso-laterally with reddish yellow spots on tergites 3–4. ♀♀: ground vestiture of tergites 3 and 4 recumbent or at most half erect.

4 Key to the north European species of *Myxexoristops*

M. arctica keys out from the other north European species of *Myxexoristops* using the following key modified from Tschorsnig & Herting 1994: 58–59. Confirmatory features are added within square brackets.

1 Parafrontal without outer orbital setae (♂♂). **2**
– Parafrontal with 2 or 3 proclinate outer orbital setae (♀♀). **7**

2 First flagellomere 5.0–6.5 times as long as pedicel, 3.0–5.5 times as wide as parafacial at its narrowest point. Face distinctly longer than frons. [Tergites 4 and 5 each covered with pruinosity in their anterior $^1/_2$–$^2/_3$. Black lateral longitu-

dinal thoracic stripe before the suture diffuse, exceeding the level of insertion of the posteriormost inner post-humeral seta. Palpus yellow to brown. Wing with second costal section bare ventrally or at most with a single black setula.]. . . . . ***M. bicolor***

– First flagellomere 3.0–4.5 times as long as pedicel, 1.5–2.8 times as wide as parafacial at its narrowest point. Face about as long as frons. **3**

3 Tibiae yellow or brownish yellow, except darkened ventrally in its basal $^1/_3$. Mid tibia with 2 anterodorsal setae. First flagellomere 3.5–4.5 times as long as pedicel. . ***M. bonsdorffi***

– Tibiae black or evenly dark brown. Mid tibia with 1 anterodorsal seta (rarely 2). First flagellomere 3–4 times as long as pedicel. **4**

4 Second costal section and often also third ventrally with some minute black setulae, which are as strong as the corresponding setulae of the first costal section (rarely second costal section with only a single seta). Tergite 3 with a band of pruinosity in anterior $^4/_5$. Scutellum reddish or yellow on the extreme tip. Tergite 3 without reddish brown lateral spot. [Facial ridge above the vibrissa with setulae and setulose hairs on lower $^1/_3$–$^2/_5$.]. . . . . ***M. stolida***

– Second costal section ventrally without minute black setulae, or if rarely present then only visible at higher magnification and distinctly smaller than corresponding setulae of first costal section. Tergite 3 with a band of pruinosity in anterior $^2/_3$ (rarely $^4/_5$). Scutellum differently coloured. Tergite 3 with or without reddish lateral spot. **5**

5 Facial ridge with some setae and setulose hairs on lower $^1/_5$–$^1/_3$, length of this row less than half the length of palpus. Palpus not widened towards tip. Scutellum broadly yellow, with yellow colouration along posterior edge extended to the basal seta. Tergite 3 usually with distinct reddish spot laterally. [Lateral longitudinal thoracic stripes before the suture well defined and ending wedge-shaped close to the insertion of the strong post-humeral setae.]. . . . . ***M. abietis***

– Facial ridge with setae and slender hairs on lower $^1/_3$–$^1/_2$, length of this row at least half the length of palpus. Palpus distinctly widened (clavate) in about apical half. Scutellum normally entirely black, but sometimes in *arctica* with a minute reddish brown spot at the extreme tip. Tergite 3 laterally usually without a reddish brown spot (an indistinct spot sometimes present in *arctica*). **6**

6 Black lateral longitudinal thoracic stripes before the suture exceeding insertion of the posteriormost inner post-humeral setae. Frons somewhat projecting (Fig. 2); parafacial at level of antennal insertion 0.5–0.6 times as wide as small diameter of eye. Parafrontal area with an additional row of setae parallel to the frontal setae; the anterior setae in this row stronger than those at vertex and almost $^2/_3$ as long as the strongest frontal seta. Scutellum entirely black. Tergite 4 usually with 4–6 median discal setae. Terminalia as in Figs. 4, 7–9, 11. Cerci in dorsal view long and slender, approximately 6 times as long as broad at midpoint; slightly enlarged shortly before apex, narrowly separated in their apical $^2/_5$–$^1/_2$. . . . . ***M. blondeli***

– Black lateral longitudinal thoracic stripes before the suture slightly diffuse, ending wedge-shaped at level of the posteriormost inner post-humeral setae. Frons not projecting (Fig. 1); parafacial at level of antennal insertion about 0.4 times as wide as small diameter of eye. Parafrontal area without a row of differentiated parafrontal setae but with setulose hairs subequal to those at vertex. Tergite 4 with 2(–4) median discal setae. Scutellum entirely black or sometimes with a small reddish brown spot at apex. Terminalia as in Figs. 3, 5–6, 10. Cerci in dorsal view short, approximately 3.5 times as long as broad at midpoint; apical half in dorsal view almost parallel sided, separated from each other by a well defined apical cleft that is about $^2/_5$ as long as the basal suture. . . . . ***M. arctica***

7 Abdomen usually with expanded yellow colouration dorsolaterally and ventrally, but tergite 3 at least with a distinct lateral spot. Tibiae usually light brown-yellow. Ground vestiture on tergites 3 and 4 recumbent, but erect between median marginal and discal setae. **8**

– Abdomen entirely black or tergite 3 at most with a small reddish brown lateral spot. Tibiae black or evenly brown, but if sometimes light brown (in *abietis*) then the ground vestiture on tergites 3 and 4 recumbent also between median marginal and discal setae. [Mid tibia usually with 1 anterodorsal seta.]. **9**

8 Coxae and trochanters yellow under the greyish white pruinosity; scape and pedicel yellow in part. Abdomen entirely yellow ventrally, with distinct lateral yellow colouring in dorsal view. Tergites 3–5 with pruinosity covering anterior $^1/_2$–$^2/_3$ of each segment. Palpus yellow. Second costal section ventrally sometimes with a single minute black setula. Claws of fore leg a little shorter than $^1/_2$ the length of tarsal segment 5. Mid tibia with 1 anterodorsal seta. . . . . ***M. bicolor***

– Coxae, trochanters, scape and pedicel black. Ventral side of abdomen yellow to a varying extent, but at least tergite 5 and usually also a ventral medial stripe black; yellow abdominal colouring not clearly visible in dorsal view. Tergites 3–5 with pruinosity covering anterior $^5/_6$–$^7/_8$ of each segment. Palpus brownish yellow to black. Second costal section bare ventrally. Claws of fore leg longer than $^1/_2$ the length of tarsal segment 5. Mid tibia with 2–3 anterodorsal setae. . . . . ***M. bonsdorffi***

9 Second costal section and often also third ventrally with some minute black setulae, which are as strong as the corresponding setulae of the first costal section (rarely only a single seta present on second costal section). Tergites 3–5 densely covered by a greyish, yellow or golden yellow pruinosity in the anterior $^4/_5$ of each segment. Scutellum reddish or yellow only at extreme tip. Tergite 3 laterally without a pair of reddish brown spots. Facial ridge above the vibrissa with some setulae and setulose hairs in lower $^1/_3$–$^2/_5$. . . . . ***M. stolida***

– Second costal section ventrally without setulae, or if rarely present then only visible at higher magnification and also distinctly smaller than corresponding setulae of the first costal section. Tergites 3–4 with pruinosity covering the anterior $^2/_3$–$^4/_5$ of each segment, on tergite 5 at most covering anterior $^3/_4$. Scutellum black or reddish brown at extreme tip. Tergite 3 laterally with or without a pair of reddish brown spots. Facial ridge above the vibrissa with some setulae and setulose hairs in lower $^1/_5$–$^1/_2$. **10**

10 Abdominal ground vestiture on tergites 3 and 4 recumbent also between median marginal and discal setae. Scutellum more or less broadly reddish yellow at tip. First flagellomere 3.4–4.0 times as long as pedicel. Tergite 5 with pruinosity in anterior $^2/_3$–$^3/_4$. [Lateral longitudinal thoracic stripes before suture well defined and ending wedge-shaped close to insertion of the strong posthumeral seta.]. . . . . ***M. abietis***

– Abdominal ground vestiture on tergites 3 and 4 recumbent, but erect between median marginal and discal setae. Scutellum usually entirely black, rarely with a small brownish spot at tip. First flagellomere 2.8–3.6 times as long as pedicel. Tergite 5 with pruinosity in anterior $^2/_5$–$^2/_3$. **11**

11 Black lateral longitudinal thoracic stripes before suture exceeding insertion of posteriormost inner posthumeral seta; black lateral thoracic stripe behind suture strongly narrowing and ending close to the posteriormost intra-alar seta. Frons projecting; parafacial at level of antennal insertion

0.5–0.6 times as wide as small diameter of eye diameter. Scutellum entirely black. . . . . ***M. blondeli***

– Lateral longitudinal thoracic stripes before suture diffuse, ending wedge-shaped at level of posteriormost inner posthumeral seta; black lateral thoracic stripe behind the suture insignificantly narrowing, extending backwards to the level of the posteriormost dorsocentral seta. Frons slightly projecting; parafacial at level of antennal insertion about 0.4 times as wide as small diameter of eye. Scutellum entirely black or with a small reddish brown spot at tip. . . . . ***M. arctica***

5 Notes on some types of *Myxexoristops* species

Tachina diligens Zetterstedt, 1844
[ZETTERSTEDT 1844: 1122]

The lectotype and a paralectotype are available in the Diptera Scandinaviae collection, drawer 21 [MZLU].

The lectotype bears the following labels: green tag // *T. diligens* / ♀ Naes Norv. (handwritten ZETTERSTEDT label) // *Phebellia* ♀ / *strigifrons* Zett. / B. HERTING det. / Lectotype *diligens* // 1981 / 512.

The paralectotype (= misassociated specimen of *Myxexoristops*) is labelled as follows: green tag // BERGE ad ALSEN / Jemtl. / 8/8 40 (printed) // 1981 / 513 // *Myxexoristops* / *blondeli* R. D. ♀ / B. HERTING det. // Paralectotype ♀ / *Tachina diligens* / Zetterstedt, 1844 / des. BERGSTRÖM 2006 // *Myxexoristops* ♀ / *arctica* (Zetterstedt) / C. BERGSTRÖM det. 2006.

The nominal species *T. diligens* was based on two females. In the original description (ZETTERSTEDT 1844: 1122–1123) wrote: "Hab. in Scandinavia boreali; 8 Jul., 8 Aug., duo specimina mihi obvia; scilicet unum in Jemtlandia ad diversorium Berge in Alsen, & alterum in Norvegia ad Næs Værdaliæ lectum.". RINGDAHL (1934: 268) regarded *T. diligens* as a synonym of *Exorista cincinna* Rondani, 1859. This opinion was repeated by RINGDAHL (1945: 27), but later (RINGDAHL 1952: 132) he changed the name to *Exorista honesta* (Robineau-Desvoidy), which is a junior synonym of *Tlephusa cincinna* (Rondani). MESNIL (1954: 328) followed RINGDAHL and treated *Tlephusa diligens* (Zetterstedt) as valid with *E. cincinna* and *T. honesta* as synonyms.

Identity: I have examined the lectotype of *Tachina diligens* and agree that it is a junior synonym of *Phebellia strigifrons* (Zetterstedt, 1838) as it was already found out by HERTING (1982: 4) and fixed by his lectotype designation. The misassociated paralectotype specimen, however, represents *Myxexoristops arctica* and not *M. blondeli* as it was presumed by HERTING (l. c.). The abdomen of this specimen possesses a pair of small reddish brown lateral spots on tergite 3 which is not a suitable character for *M. blondeli*.

Tachina porcula Zetterstedt, 1859
[ZETTERSTEDT 1859: 6103]

T. porcula was described from a single ♀. In his original description ZETTERSTEDT wrote: "Hab. in Scania rarissime: ad Lindholmen d. 29 Jul. 1858 ♀ unica, *Roth*.". The holotype of *porcula* cannot be located and is apparently lost.

LUNDBECK (1927: 339–341) used the name "*Zenillia porcula* (Zett.?) Pand." and noted as a remark: "I have kept the name *porcula*, but whether the species is *porcula* Zett. cannot be decided, for according to a communication from Dr. BENGTSSON *porcula* is not found in ZETTERSTEDT's collection. – After a communication from Dr. VILLENEUVE is *stolida* Stein l. c. a variety of the present species.". RINGDAHL (1945: 34) examined the holotype of *T. porcula* that at that time apparently existed in the ROTH collection drawer 13 (2) in Lund. He adopted the name *porcula* as a valid species in the combination suggested by LUNDBECK, i. e. *Zenillia porcula* with *petiolinervis* as a junior synonym and with *stolida* as a probable junior synonym. This opinion was repeated by RINGDAHL (1952: 132) but was not followed by other authors. MESNIL (1955: 446) treated *porcula* in synonymy with his concept of *M. blondeli* which however also included *M. stolida*.

HERTING (1984: 65) synonymized *porcula* with *blondeli*. He possibly based the synonymy solely on the character of the greyish pruinosity, "griseo-cinerea, opaca", mentioned in the original description. This variable character alone is definitely not sufficient for a safe recognition of *blondeli*. The original description also says: "palpis summo apice luteis", which means that the palpi have yellow tip. Females of *M. stolida* examined by me all have yellow palpi at least at the extreme tip, whereas females of *M. blondeli* all have entirely black palpi, i. e. yellow palpi indicate *M. stolida*.

Identity: The current listing of *Tachina porcula* as a synonym of *Myxexoristops blondeli* (HERTING 1984: 65) is probably wrong and I agree with RINGDAHL (1945) that *porcula* is most probably conspecific with *stolida*. *M. porcula* would then have priority. But as the type is lost and the identity of the species cannot be proved with absolute certainty, the name *M. porcula* should better be treated as nomen dubium than to replace the long-accepted name *M. stolida* (see also below under *T. petiolinervis*).

Tachina petiolinervis Zetterstedt, 1859
[ZETTERSTEDT 1859: 6126]

The holotype is still available in the ROTH collection, drawer 13 [MZLU]. It is labelled as follows: "Lhn / 9/7 // *T. petioli-* / *nervis* Zett. / n. sp. ♂ (handwritten ZETTERSTEDT label) // Holotype / *T. petiolinervis* Zett. / B. HERTING det. // *Myxexoristops* / *stolida* Stein ♂ / B. HERTING det.".

T. petiolinervis was described from a single ♂. In the original description ZETTERSTEDT (1859) wrote: "Hab. in Scania rarissime: ad Lindholmen d. 9 Jul. 1856 marem unicum invenit *Roth*.". RINGDAHL (1945: 29, 34) regarded *M. petiolinervis* as a junior synonym of *T. porcula*, but this opinion was not followed by HERTING (1984: 65) who treated *M. petiolinervis* as a junior synonym of *M. blondeli*. The name *petiolinervis* alludes to the fact that that wing cell r_{4+5} of the holotype possesses a petiole (which is about as long as crossvein r-m). This character is aberrant and not useful in the classification of *Myxexoristops*.

Identity: I have examined the holotype and it is conspecific with *Myxexoristops stolida* (Stein, 1924). *M. petiolinervis* (Zetterstedt, 1838) is the older name and would normally have priority, but to avoid unnecessary changes of long-accepted names, Art. 23.9. was introduced in the 1999 edition of the ICZN. To maintain the stability of the name *M. stolida* it is stated herewith that according Art. 23.9.1.1. *M. petiolinervis* was not used as a valid name after 1899, and that according to Art. 23.9.1.2. *M. stolida* has been used as a valid name in more than 25 works of more than 10 authors in the preceding 50 years, encompassing a spam of more than ten years. The name *M. stolida* has been used in various papers on the biology of Tenthredinidae (e. g. EICHHORN & PSCHORN-WALCHER 1978), host catalogues (e. g. SHIMA 1999), keys (e. g. TSCHORSNIG & HERTING 1994), many regional faunas (e. g. VAŇHARA et al. 2004), etc. *M. petiolinervis* (Zetterstedt, 1838) hence becomes the status of a nomen oblitum.

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Manuscript received: 15.VII.2007, accepted: 31.X.2007.

A new species of *Plesina* Meigen (Diptera: Tachinidae) from the Mediterranean

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Abstract

A new tachinid species (Diptera: Tachinidae), *Plesina nigroscutellata* **n. sp.** from Sardinia, Spain and Crete, is described. The main features that distinguish the new species from the similar *Plesina claripennis* Mesnil, 1953 are the different abdominal proportions, the darker colour, and a more distinct pruinescence.

Keywords: Tachinidae, *Plesina*, Sardinia, Spain.

Zusammenfassung

Eine neue Raupenfliegen-Art (Diptera: Tachinidae), *Plesina nigroscutellata* **n. sp.** aus Sardinien, Spanien und Kreta, wird beschrieben. Die neue Art unterscheidet sich von der ähnlichen *Plesina claripennis* Mesnil, 1953 hauptsächlich durch andere Abdominalproportionen, dunklere Färbung und deutlichere Bereifung.

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1 Introduction

The tachinine genus *Plesina* Meigen, 1838 was previously known from eight species:

P. phalerata (Meigen, 1824) from France, Spain and Morocco (Czerny & Strobl 1909, Wainwright 1933, Villeneuve 1934, Kugler 1978, Herting 1984, Herting & Dely-Draskovits 1993, Tschorsnig et al. 1997);
P. fascipennis (Wiedemann, 1830) from Sudan (Kugler 1978);
P. claripennis Mesnil, 1953 from Egypt (Sinai), Israel [including Cisjordania] and Syria (Kugler 1978, Herting 1984, Herting & Dely-Draskovits 1993); the records from Crete (Herting 1984, Herting & Dely-Draskovits 1993) and Spain (Tschorsnig et al. 1997) turned out to be erroneous (see below);
P. africana Kugler, 1978 from Nigeria (Kugler 1978);
P. deserticola Kugler, 1978 from Israel and Egypt (Sinai) (Kugler 1978);
P. nepalensis Kugler, 1982 from Nepal (Kugler 1982);
P. asiatica Richter, 1988 from Tajikistan (Richter 1988);
P. zimini Richter, 1991 from Uzbekistan (Richter 1991).

The genus is characterized by the following combination of external morphological features: male frons very narrow, without orbital setae, frontal stripe very narrow; female frons about as wide as or wider than an eye in dorsal view, with 2–4 proclinate or lateroclinate orbital setae; parafacial with a row of short and robust proclinate setulae; back of head with at least a few pale hairs ventrally; fore coxa elongated, about half as long as fore femur; one katepisternal seta; anterior and posterior lappets of posterior spiracle about equal in size; postmetacoxal area entirely or partly sclerotized; wing cell r_{4+5} long petiolate; abdominal tergites usually consisting of two different parts (except in *P. deserticola* and *P. zimini*).

Plesina flies live close to the ground and do not visit flowers; this behaviour is probably the reason why individuals are normally only rarely collected. *Plesina claripennis* and *P. deserticola* have been observed running on the ground and on rocks or flying short distances close to the ground, often beneath trees (Kugler 1978, 1982; Freidberg pers. comm. 2007); specimens of *P. phalerata* were collected in Spain by the second author while they were sitting or running on large stones on a steep slope (see Tschorsnig et al. 1997).

A new Mediterranean species of *Plesina* is described below, based on six specimens. The female from Crete was (mis-)identified by Herting as *Plesina claripennis*, and subsequently recorded under this name in his catalogues (Herting 1984, Herting & Dely-Draskovits 1993) from Greece. Also the two Spanish females were recorded under the erroneous name *P. claripennis* by Tschorsnig et al. (1997). The finding of one male and two females from Sardinia enabled us to show that the dark specimens are not a simple colour variation of *P. claripennis* but belong to a separate species, with clear-cut morphological differences.

No preparation was made of the genitalia of the holotype of *P. nigroscutellata* n. sp. to avoid damage of this single male specimen. The species can easily be distinguished from other *Plesina* by its external morphology

(see key in chapter 3), and variability of the male genitalia within the genus seems not very important (see figures in KUGLER 1978).

The length of the abdominal segments was measured medially in exact dorsal view; the fore margin of syntergite 1+2 is meant at the level of its anterior lateral edges.

Digital SEM images were used to show details of the fine morphology of "pruinescence" (= fine reflecting microtrichosity that looks like a thin waxy layer when viewed under low magnification).

Acronyms of depositories

CNBF Insect collection of Centro Nazionale Biodiversità Forestale, Verona, Italy
MZLU Museum of Zoology, Lund University, Lund, Sweden
MZUR Museum of Zoology, Università degli Studi di Roma "La Sapienza", Rome, Italy
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany
TAU Museum of Zoology, Tel-Aviv University, Israel

Acknowledgements

The first author is grateful to AMNON FREIDBERG (TAU), who enabled him to study the valuable material preserved in his institution and for his hospitality during a recent visit to Tel Aviv, and to FRANCO MASON (CNBF) for making the research work in Sardinia possible. Thanks are due to DANIEL WHITMORE (CNBF) for help with the English language, and to CHRISTER BERGSTRÖM (Uppsala) and JOACHIM ZIEGLER (Berlin) for the review of the manuscript. The second author is grateful to ROY DANIELSSON (MZLU) for the loan of his specimen from Crete.

2 Description of *Plesina nigroscutellata* n. sp.

Material

Holotype (♂): Italy, Sardinia, (Carbonia-Iglesias), Iglesias, near Colonia Benek, 636 m, UTM 32 S 04662391 4355441, 27.VI.–11.VII.2006, Malaise trap, leg. G. CHESSA (MZUR).

Paratypes: 2 ♀♀, same data as holotype, but 13.–27. VI.2006 (CNBF). – 1 ♀, Spain, Prov. Salamanca, Villar de Ciervo, Las Coronas, 720 m, 22.VI.1994, leg. H.-P. TSCHORSNIG (SMNS). – 1 ♀, same data as before, but 28.VI.1995 (SMNS). – 1 ♀, Greece, Crete, 2 km S Malia, near pump station, 15.V.1979, leg. R. DANIELSSON (MZLU).

The Sardinian and the Spanish specimens were collected in Malaise traps installed directly in or in the vicinity of *Quercus ilex* forests.

Etymology

The name "nigroscutellata" is derived from the black scutellum.

Description

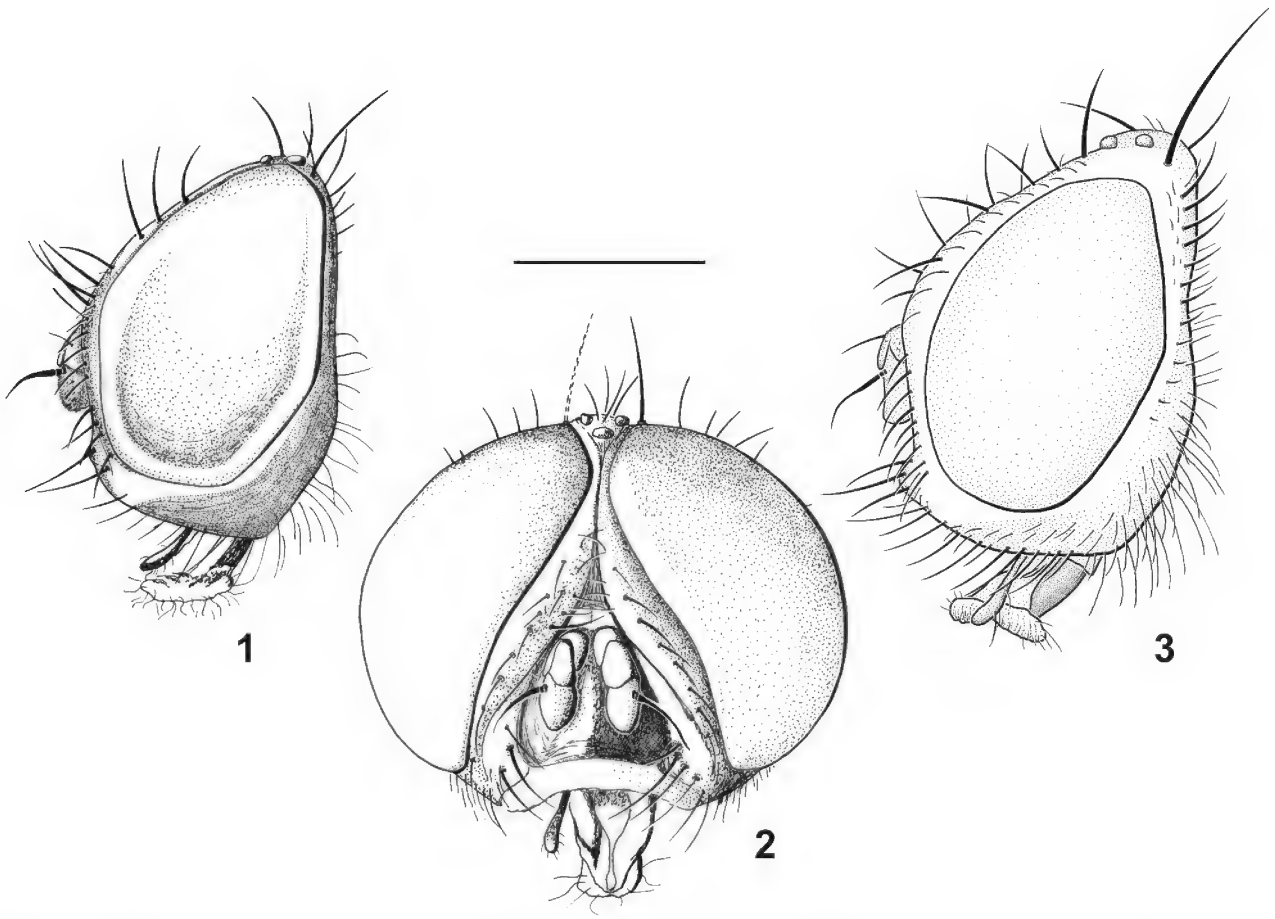
Male:

Colour: Head black; first and second antennal segment black or dark brown; palpus mainly brown, slightly yellowish at tip. Thorax entirely shiny black. Halter basally yellowish, shading into brown distally. Lower calypter smoky with a brown margin. Tegula dark brown, basicosta reddish-brown. Wing predominantly hyaline, slightly infuscate to blackish anterobasally. Legs dark; trochanters yellowish, fore coxa reddish on anterior surface, mid and hind femora slightly reddish near trochanter. Abdomen bicoloured: syntergite 1+2 and tergite 3 predominantly yellow with a medial sub-triangular dark spot (concave anterior part of those tergites dark), lateroventral sides of tergite 4 yellow (dorsally largely black) and lateral margin of tergite 4 yellowish.

Pruinescence: Fronto-orbital plate and parafacial covered with light grey pruinescence. Thorax with a very light grey pruinescence laterally (dorsally shiny black). Abdominal syntergite 1+2 and tergite 3 with a very light pruinescence on the concave anterior part (visible in posterior view), and dense pruinescence on the convex posterior part (visible in anterior view) (Figs. 8, 13). Abdominal tergites 4 and 5 with a slight pruinescence (visible in anterior view) due to relatively scattered and erect microtrichia (Fig. 7).

Head (Figs. 1–4): Hemispherical shape. Eye bare. Frontal stripe very narrow, practically extinct in front of anterior ocellus. Frons at its narrowest point 0.08 times as wide as an eye in dorsal view. Inner vertical seta about 0.3 times vertical diameter of eye, outer vertical seta not differentiated. Ocellar setae present, proclinate. No upper reclinate orbital setae. Height of facial ridge about $^1/_2$ the length of the frons; antenna inserted below level of middle of eye. Fronto-orbital plate without proclinate orbital setae. Lowermost frontal bristle at level of antennal base. Parafacial strongly narrowed ventrally, at its narrowest point, when seen in profile, 0.4 times as wide as third antennal segment, with a row of stout, proclinate black setulae along its whole length. Facial ridge with one or two setulae above the vibrissa. Vibrissa arising at level of lower facial margin, the latter slightly visible in lateral view. Third antennal segment about as long as second antennal segment. Arista bare, thickened on about basal $^1/_4$; second aristomere as long as wide. Gena, when seen in profile about 0.1 times vertical diameter of eye; genal dilation triangular, short. Back of head with pale hairs ventrally. Prementum slightly longer than wide. Palpus slightly longer than prementum, enlarged apically.

Thorax: Prosternum and proepisternum bare. Postpronotum with 2 setae. Scutum with 1+0 acrostichal setae; 2+2–3 dorsocentrals; 1–2 posthumerals; 1+0–1 intra-alars; 0–1 postsutural supra-alar setae (first postsutural supra-alar seta, if present, shorter than notopleural setae); 2 notopleurals; postalar callus with 2 setae. One katepisternal seta. One short anepimeral seta. Katepimeron bare. Scutellum with 2 pairs of marginal setae (basals and divergent apicals) and 4 pairs of recumbent discal setulae. Mediotergite bare below lower calypter. Anterior and posterior lappets of posterior spiracle about equal in size. Meron with 1–3 setae. Postmetacoxal area entirely sclerotized.



Figs. 1–3. *Plesina nigroscutellata* n. sp. – **1–2**. ♂ head, lateral and frontal view. **3**. ♀ head, lateral view. – Scale: 0.5 mm.

Wing (Fig. 6): Second costal portion bare ventrally. Costal bristle not differentiated from the other costal setae. R_1, base of R_{4+5}, and CuA_1 bare. Cell r_{4+5} with a petiole 1.10–1.15 times as long as postangular section of M.

Legs: Fore tibia without posterior setae; preapical anterodorsal seta about as long as preapical dorsal seta. Mid tibia with 1 anterodorsal seta, 1 ventral seta, and 2 posterior setae. Hind tibia with 2 anterodorsal setae, 2 posterodorsal setae, and 2 dorsal preapical setae; preapical posteroventral seta nearly as long as preapical anteroventral seta. Claws about half as long as fifth tarsal segment.

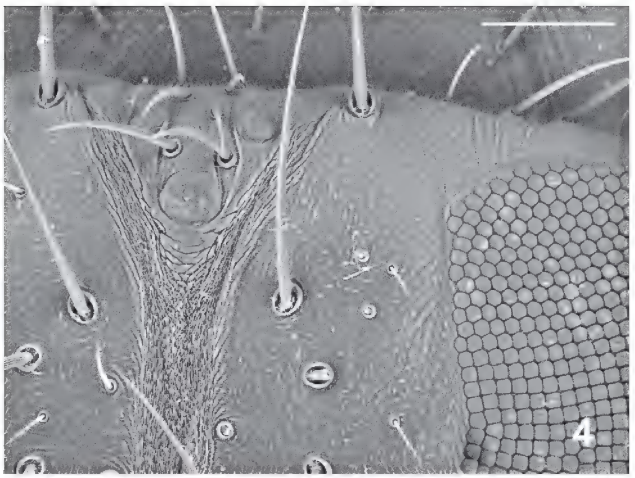
Abdomen: Tergites 1+2 and 3 differentiated into a slightly concave and bare anterior part, and a more or less convex posterior part with two rows of robust recumbent setulae (as in Figs. 8, 13). Tergites 4 and 5 with the normal recumbent setulae. Syntergite 1+2 with 2 strong median marginal bristles; middorsal excavation confined to about anterior $^1/_4$ of that segment. Tergite 3 with 4 strong marginal bristles and a small additional seta inserted next to the lateral bristle. Tergite 4 with 2 pairs of median marginal bristles; distance of the median pair to the hind margin about $^2/_5$ the length of that segment. Tergite 5 with a row of 4 bristles (weaker than on tergites 3 and 4) slightly behind the mid length of that segment. Combined dorsal length of tergites 1–3 1.16 times as long as combined length of tergites 4–5. Postabdomen not dissected (see introduction).

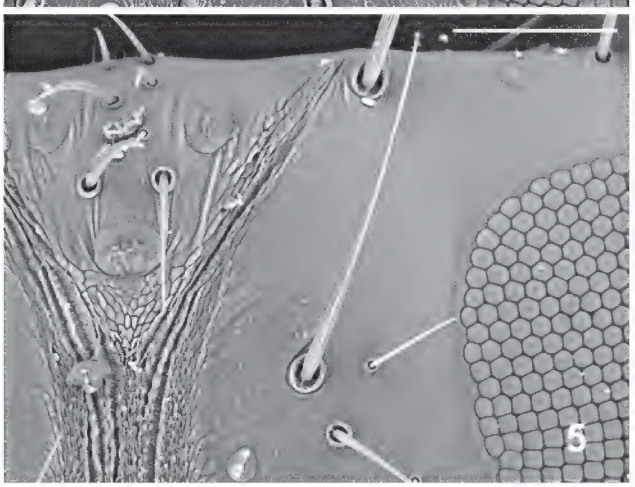
Body length 3.0 mm.

Females differ from male as follows:

Colour: Posteroventral fourth of head yellowish to black; antenna, face and gena brown in one specimen from Spain; palpus yellowish to brown, femora more or less reddish basally and anteroventrally; abdomen entirely black (in the Crete specimen), or convex posterior part of syntergite 1+2 dark reddish dorsolaterally and a common lateralventral spot of tergites 1–3(–4 in one specimen) yellow.

Pruinescence: Light pruinescence on frons visible in posterior view (not in the Crete specimen), due to scattered microtrichia as shown in Fig. 4; thorax with a very light grey pruinescence laterally, antero- and posterodorsally.





Figs. 4–5. *Plesina* spp., ♀ frons. – **4**. *P. nigroscutellata* n. sp. **5**. *P. claripennis*. – Scale: 0.1 mm.

Head (Figs. 3–4). Eye smaller; frons at its narrowest point 1.24 times as wide as an eye in dorsal view in the Crete specimen, 0.90–1.04 times in the other specimens (which were dried from alcohol). Inner vertical seta about 0.6 vertical diameter of eye. Frontal stripe as wide as $^1/_3$–$^2/_5$ of a parafrontal. One reclinate upper orbital seta present. Fronto-orbital plate with a row of 2–4 proclinate orbital setae (the posterior one slightly lateroclinate).

Scutum with 1 + 0–2 acrostichal setae.

Base of R_{4+5} bare or with 1–2 minute setulae (in the Spanish specimens).

Pulvilli of fifth fore tarsal segment absent, fore claws minute; claws of mid and hind legs about as long as $^1/_3$ of fifth tarsal segment.

Tergite 3 with a pair of median marginal bristles. Combined dorsal length of tergites 1–3 0.9–1.1 times as long as combined length of tergites 4–5 (Figs. 8, 13). Postabdomen without peculiarities.

Body length 3.6–4.5 mm.

Fig. 6. *Plesina nigroscutellata* n. sp., wing.

3 Differential diagnosis

The newly described species *Plesina nigroscutellata* n. sp. can be separated from the other species of the genus *Plesina* as follows:

1 Wing patterned, with dark transversal bands or spots (compare figs. 2, 6, 8 of Kugler 1978, figs. 5 and 7 of Kugler 1982, and fig. 4(3) of Richter 1988). . . . . other species of *Plesina*

– Wing unpatterned (Fig. 6; figs. 12 and 18 of Kugler 1978). **2**

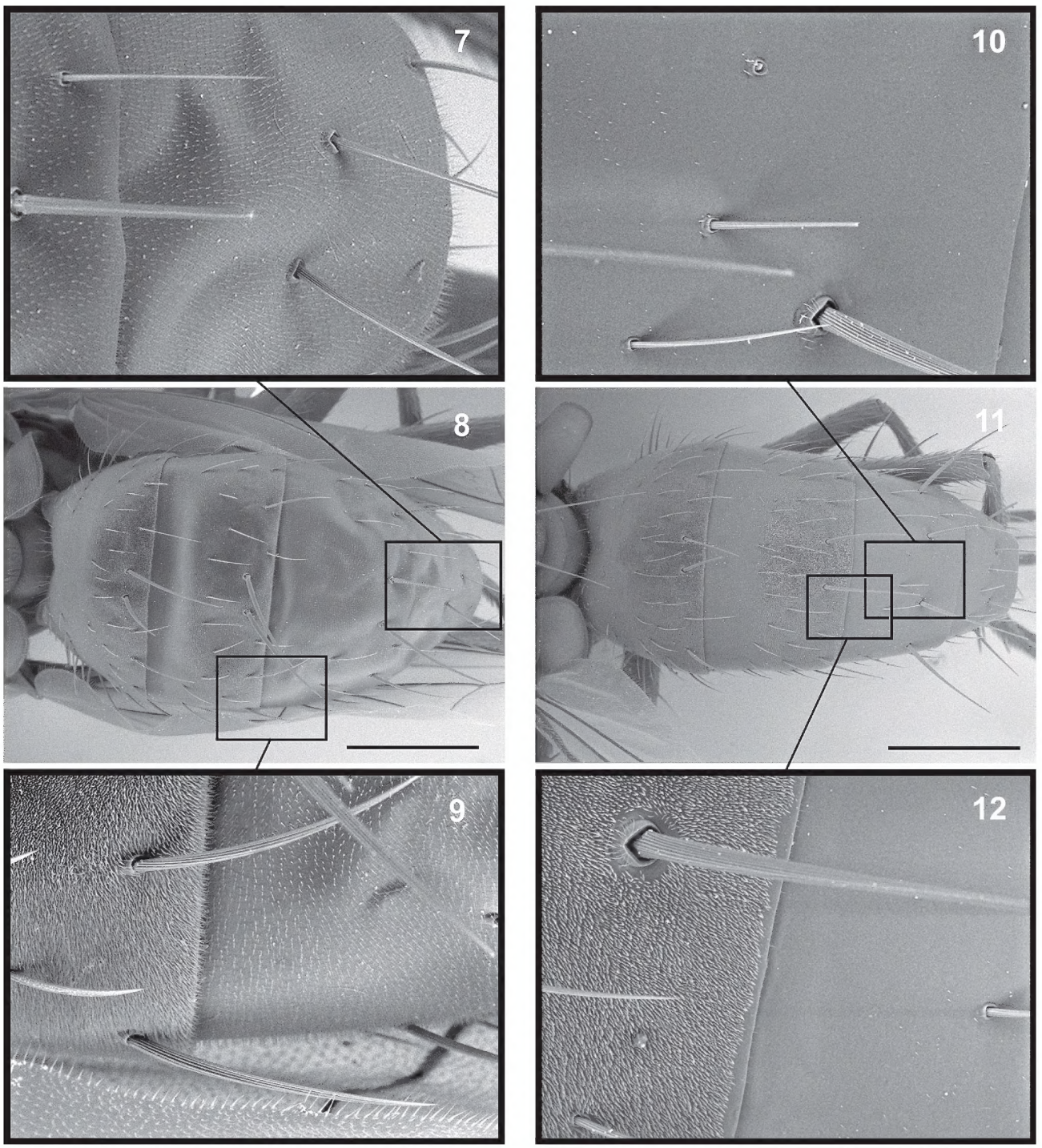
2 Abdominal tergites 1+2 and 3 of unique structure, not consisting of two different parts; abdomen covered with the normal recumbent setulae; at least tergites 1–4 with small spots of pruinescence (in posterior view). Thorax with dense pruinescence (in anterior view). . . . . ***P. deserticola*** and ***P. zimini***

– Abdominal tergites 1+2 and 3 each differentiated into a slightly concave and bare anterior part and a more or less convex posterior part with rows of recumbent setulae (Figs. 8, 11, 13–14). Thorax at most with very weak pruinescence. **3**

3 Combined dorsal length of tergites 1–3 about 1.7–2.0 times as long as combined length of tergites 4+5 in ♂ (see fig. 3 of Kugler 1978), 1.5–1.6 times in ♀ (Figs. 11, 14). Thorax including scutellum more or less yellow (in darkened specimens at least the posterior margin of the scutellum yellow), the latter usually with 2 discal setulae. Halter usually yellow. Tegula yellow. Legs usually predominantly yellow (very rarely largely dark brown). Margin of lower calypter fine, yellowish or light brown. Abdominal tergites 4 and 5 entirely shiny, without any pruinescence (Figs. 10–12). – ♀: Fifth fore tarsal segment 2.1–2.5 times as long as wide; frons entirely shiny, also in posterior view (Fig. 5). – Egypt, Israel, Syria. . . . . ***P. claripennis***

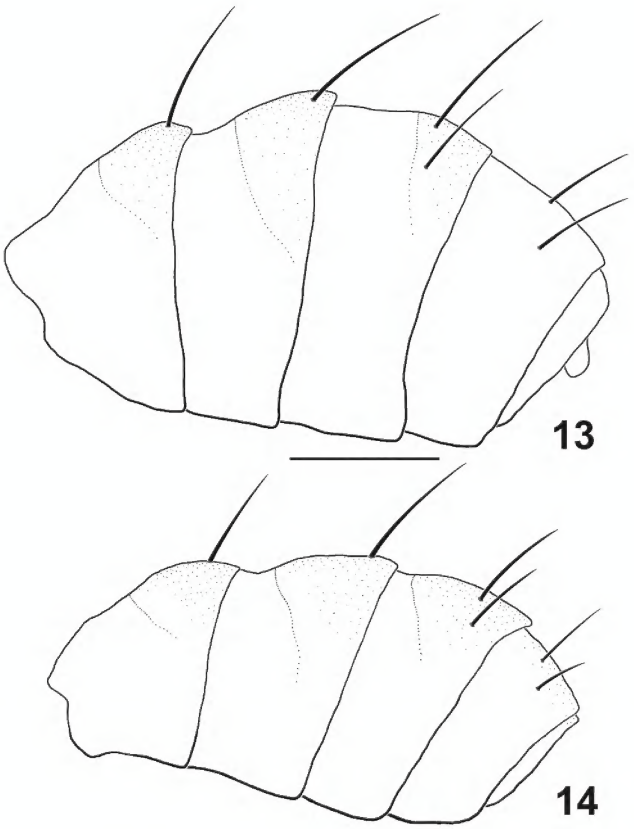
– Combined dorsal length of tergites 1–3 about 1.2 times as long as combined length of tergites 4+5 in ♂, 0.9–1.1 times in ♀ (Figs. 8, 13). Thorax including scutellum entirely black, the latter with 3–5 discal setulae. Knob of halter brown. Tegula dark brown. Legs predominantly dark brown or black. Lower calypter with a coarse dark margin. Abdominal tergites 4 and 5 with slight pruinescence (best visible in anterior view) (Figs. 7–9). – ♀: Fifth fore tarsal segment 1.8–2.0 times as long as wide; light pruinescence on frons usually visible in posterior view (Fig. 4). – Spain, Sardinia, Crete. . . . . ***P. nigroscutellata* n. sp.**

Kugler (1978), in his description of the females of *Plesina claripennis*, noted: "variable in colour, from nearly



Figs. 7–12. *Plesina* spp., ♀ abdomen, dorsal view. – **7–9**. *P. nigroscutellata* n. sp. **10–12**. *P. claripennis*. – Scale: 0.5 mm.

entirely shiny yellow to almost entirely black". The examination by the first author of more than 300 specimens of *P. claripennis* preserved in TAU revealed that even in darker specimens the scutellum has a narrow yellow posterior rim, that the legs are at least partly yellow, that the combined dorsal length of abdominal tergites 1–3 is at least 1.5 times as long as the combined length of tergites 4–5, and that the abdominal tergites 4 and 5 are always entirely shiny, without pruinescence.



Figs. 13–14. *Plesina* spp., ♀ abdomen, lateral view. – **13**. *P. nigroscutellata* n. sp. **14**. *P. claripennis*. – Scale: 0.5 mm.

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Manuscript received: 20.VI.2007, accepted: 5.XI.2007.

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